THE DEMOGRAPHY AND ECOLOGY OF THE PULMONATE LIMPET *SIPHONARIA ZELANDICA* AT KAIKOURA, NEW ZEALAND.

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by
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Beyond the ken of mortal men, beneath the wind and waves,
There lies a land of shells and sand, of chasms, crags and caves,
Where coral castles climb and soar, where swaying seaweeds grow,
And all around without a sound the ocean currents flow.....

- Graeme Base

`The Sign of the Seahorse'

CONTENTS

ABSTRACT

Siphonaria zelandica is a common intertidal pulmonate limpet in New Zealand. On the Kaikoura Peninsula, east coast of the South Island, *S.zelandica* is abundant on rocky platforms in damp crevices. This study examines the demography and ecology of *S.zelandica* at two sites on the peninsula. The distribution and abundance was examined both spatially and temporally. *S.zelandica* are found primarily in the mid tidal area with an average of 90limpets/m^2 over all sites although abundance does vary between sites. *S.zelandica* are, however, not strongly associated with any other gastropod species, although they are correlated with algae. Two size measurement methods were used to ascertain growth and mortality of *S.zelandica*, and the reproductive cycle was also determined. Growth is variable over time, being quicker in winter and spring than in summer/autumn. Growth is also variable with initial size of the animal with smaller size classes (6-10mm) growing rapidly and the larger size classes having slower growth. Mortality is greater in the larger *S.zelandica* than in small size classes and is affected by physical disturbances such as storms. Reproduction in *S.zelandica* is continuous over the year as shown by histological slides which showed that there were mature oocytes present throughout the year. There are peaks in spawning however that occur in February/March (late summer) and September/October (early spring) which indicate main spawning phases. Hatching after the eggs had been laid took between six and ten days and settlement was fairly rapid after this.

The grazing effect of *S.zelandica* on algal abundance and the effects of differing densities of limpets on intraspecific survival and growth were examined through experimental enclosures. 0.25m^2 enclosures were constructed and randomly assigned treatments at two sites. The different densities used were 0,15, 30 and 60 limpets which represent half ambient, ambient and double ambient densities and the experiment was run for twelve months. It was found that although *S.zelandica* had some effect on algal abundance at differing densities, overall they cannot reduce micro or

macroalgae by significant levels. An increase in density of the limpets had no effect on *S.zelandica* survival. Growth was significantly different between sites although there was no significant treatment effect.

Experimental enclosures were also used to examine whelk predation on *S.zelandica*. Treatments used were a series of total and half cages with 30 *S.zelandica* and either with or without whelks. The treatments were duplicated at both mid and low shore. The experiment had a two-fold nature, it indicated the level of whelk predation at different shore heights and the survival of *S.zelandica* at the different shore heights. Whelks consume reasonable numbers of limpets at both mid and low shore heights but predation is increased at the low shore. *S.zelandica* does not survive well at the low shore regardless of being protected from whelks. Oystercatcher predation was examined by observations of foraging flocks. These found that oystercatchers have a major effect on limpet populations leaving, on average, only 10% of *S.zelandica* untouched in a patch after the birds foraging session. The behaviour of the oystercatchers was unusual as they turned the limpets over but never actually consumed them.

The main conclusions of this study are that *S.zelandica* contribute to the patch dynamics of the Kaikoura shore by having both direct and indirect effects. The direct effects of *S.zelandica* are the localised population effects on algal abundance. Indirectly, *S.zelandica* are prey for both birds and whelks, which is a factor in their patchy distribution that in turn creates space for other organisms to settle.

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CHAPTER ONE

General Introduction

GENERAL INTRODUCTION

1.1 Background

The purpose of this thesis is to investigate the demography and ecology of the pulmonate limpet, *Siphonaria zelandica* at Kaikoura, New Zealand. Although limpets (both prosobranch and pulmonate) have been extensively studied worldwide (see reviews by Underwood 1979, Branch 1981, Branch 1986) there have been few studies in New Zealand. Pulmonates have been less extensively studied than prosobranchs and are often referred to as `false' limpets because, unlike their prosobranch counterparts, they possess a lung and can respire aerially. *Siphonaria zelandica* are widely distributed in New Zealand and generally are found in the mid tidal region in patches mostly devoid of macroalgae. Siphonariidae is a family of limpets in the order Basommatophora but they differ from most pulmonates in that there is a secondary gill allowing the animals to respire both when submerged or emersed (De Villiers and Hodgson,1987). Siphonariids are believed to be derived from primitive stock but have made some important adaptations to their morphology, such as the secondary gill, and physiology to allow them to live in a wide range of habitats. In New Zealand there are four representatives of siphonariid limpets, *Siphonaria zelandica*, *S.australis, S.cookiana and Benhamina obliquata*. *Benhamina obliquata* and *Siphonaria zelandica are* similar in shell morphology but *Benhamina* is much larger than *S.zelandica* with smaller adult *Benhamina* ~34mm while the maximum recorded size of *S.zelandica* is 27mm (Powell 1979). Another difference between the two is that they produce completely different size and colour egg masses. *Siphonaria* occurs in large numbers on rocky mounds and platforms, often associated with dense aggregations of prosobranchs (Schiel, in prep.).

There have been many hypotheses proposed to account for the patch dynamics and distribution of organisms on rocky shores (Underwood and Denley 1984, Menge 1992,1995). Although many of these have been tested in the northern hemisphere, fewer hypotheses concerning the dynamic processes

on the intertidal shore have been getting attention in the southern hemisphere rocky intertidal. While many studies often find similarities or areas of agreement with general hypotheses, researchers are also finding some important differences. (Underwood and Denley, 1984) It is clear that ecological communities vary widely in space and time (Menge and Olson, 1990), due to differences in both the physical and biological habitat.

Limpets are important herbivores in the intertidal zone and can have large impacts on the distribution and abundance of algal species present (Menge and Sutherland 1976, Branch 1981, Cubit 1984, Underwood and Jernakoff 1984, Farrell 1988, Beovich and Quinn 1992, Liu 1993, Menge 1995). For example, the distribution and abundance of algae has been shown to vary due to height on shore, season, exposure, density of grazers and competition between and within herbivorous species. Siphonariid grazing has been studied in South Africa (Lasiak and White, 1993), Bermuda (Cook and Cook 1981) and extensively in Australia (Underwood and Jernakoff 1981, Creese and Underwood 1982, Beovich and Quinn 1992). The results of these studies varied but generally showed that high densities of *Siphonaria* reduce growth rates but do not affect mortality (Creese and Underwood,1982). High densities also show no significant effect on algal growth and density (Underwood and Jernakoff 1981, Beovich and Quinn 1992, Lasiak and White 1993). Cook and Cook (1981) examined grazing patterns of *Siphonaria* in Bermuda and found that they tend to avoid areas that they have previously grazed, but their general grazing pattern is random. There has been only one study on the ecology of *Siphonaria zelandica* in New Zealand (Jeffs, 1985) and there is also a review on grazing in New Zealand (Creese, 1988). Jeffs found that on intertidal platforms in northern New Zealand, *S.zelandica* is found only on the encrusting alga *Ralfsia verucosa*. He found that increased density of the limpets led to reduced growth rates and weights of individuals. Contrary to studies mentioned earlier where no effect on mortality was found when densities of *Siphonaria* were increased, Jeffs found that an increase in density of *S.zelandica* did cause an increase in mortality. In Australian and South African

studies, *Siphonaria* species tend to eat macroalgae but leave the basal parts of the plants intact causing a film to be found on the surrounding substrate (Underwood and Jernakoff 1982, Lasiak and White 1993). *Siphonaria zelandica* feed on both micro- and macroalgae; they posses a finer radula than do prosobranch limpets and do not scrape rock surfaces so deeply (Wong, 1980).

Population structure and life history events can greatly influence dynamic interactions. Quinn (1988a, b) found that despite the large amount of information available on intertidal limpets, little work has been done on the population dynamics and reproductive patterns of *Siphonaria* species. His conclusions were that reproductive output is directly linked to food availability in *S.diemensis* and that this leads to flexibility in the timing of spawning. In Australia, the reproductive cycle for *S.denticulata* and *S.virgulata* was established (Creese, 1980). By counting egg numbers per egg ribbon and the number of egg ribbons produced per individual, Creese found that fecundity increased with limpet size and that both species could spawn for several months of the year. Growth and mortality can be assessed in several ways but using mark-recapture methods is particularly effective on relatively sessile organisms such as limpets (Creese 1981, Quinn 1988, Treble et al.1993). Variability in growth and mortality can be closely linked to food availability, density of limpets and season. Patchiness in distribution can be caused by many factors (Hawkins and Hartnoll,1983) from initial recruitment process to physical processes (Woolcott 1973, Paine and Levin 1981) and biological limits such as food availability and density (Black 1977, Creese 1980).

Predation can greatly affect limpet abundance, with consequent effects on algal patchiness. Predation of limpets by birds and whelks has been well studied (Paine 1963, Luckens 1974, Hartwick 1976, Frank 1982, Hockey and Branch 1984, Branch and Cherry 1985, Marsh 1986, Lindberg et al. 1987, Barkai and Branch 1988, Wootton 1992, Iwasaki 1993). Predation affects the mortality of prey species, density and distribution. There can also, like grazing, be indirect

effects such as removal of limpets by a predator causing an increase in space available for other species to settle. There are some species of *Siphonaria* that develop defensive responses to predation such as homing to a fixed scar or producing toxins (Iwasaki, 1993). At Kaikoura it appears *S.zelandica* has the ability to home because prominent scars are found on the substrate into which individuals neatly fit. *S.zelandica* is believed to home along a mucus trail produced as it leaves its scar (Walsby and Morton, 1982). When these limpets move away from home scars, their foot protrudes noticeably below the shell and this combined with their weak grip on the substrate makes them easily removed by predators.

Wong (1980) examined the physiology (digestion and respiration) of *S.zelandica* in northern New Zealand but little has been done on its ecology in the South Island. As *S. zelandica* occurs in large numbers around the Kaikoura peninsula and is somewhat patchy in its distribution, its role in the intertidal community could be important. It may be an opportunistic settler that makes the most of conditions that are unfavourable to other organisms of the intertidal or, more likely, *S.zelandica* may be an integral part of the ecology on intertidal platforms due to it occupying large spaces and its grazing effects on algae.

1.2 Study Sites

The shoreline of New Zealand is approximately 10, 000 kilometers long (Kirk 1977). There is no data on how much of this consists of rocky shore but Emery and Kuhn (1982) estimated that eighty percent of the worlds coastline is rocky and a similar figure for New Zealand seems likely. On the East Coast of the South Island, there are three peninsulas with the smallest of them being Kaikoura. It is located between 42°25'11" and 42°23'22" south latitudes and at 173° 42' longitude east. Projecting 4.5 km out from the coastline (Pirker, 1992) the Peninsula is compact in shape with an intertidal area of 0.77 km^2 (Kirk 1977). The two main rock types around the Peninsula are the tightly faulted and folded limestone and the smoother platforms of softer tertiary mudstone (Stephenson and Kirk, 1996).

The Peninsula is situated in a unique area as the continental shelf comes within five kilometres of shore, rising up from the southern extremity of the Hikurangi Trough from a depth of more than 2300m. There is a second trench lying parallel to the coast south of the Peninsula (Rasmussen, 1965), known as the Kaikoura Canyon which is between 1000 and 1500m deep. Between the Haumuri Bluffs and South Bay the edge of the continental shelf is never more than 2km offshore.

The water around the peninsula is strongly affected by the north flowing `Southland Current' and the south flowing `East Cape Current', which combine to form the Subtropical Convergence off the Kaikoura Peninsula. The Southland Front has two `arms', one turning offshore at Kaikoura and one extending further north close to shore (Heath, 1985). Heath's 1985 review of the physical oceanography around New Zealand comments on the fact that tidal currents are stronger than any other flow component. On the open coast, tidal currents are at a maximum and move anticlockwise at high tide and clockwise at low tide. Around Kaikoura the tidal crest can differ markedly from those actually observed due to the prevailing winds (Rassmussen, 1965). The prevailing wind is from the south and south - west in the winter which causes tides to be higher on the south-western face of the Peninsula and lower on the north-eastern side as well as making the tides earlier. In summer the prevailing wind is north easterly and causes the opposite effect. The positioning of the Kaikoura Peninsula in relation to the northern coast to Cape Campbell means that during summer the northerly winds generate cold, nutrient -rich upwellings. The Kaikoura Peninsula (Figure 1.1) consists of a mixture of exposed headlands and more sheltered bays. The south side of the Peninsula generally receives the rougher seas and stronger winds. This, combined with the oceanic currents, often causes a near shore band of murky water.

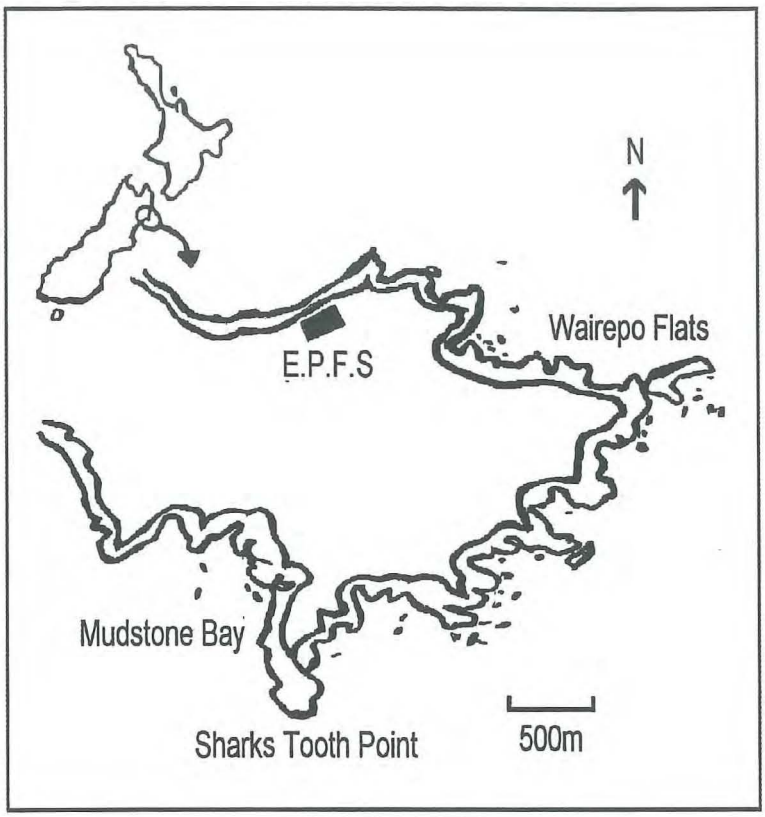


Figure 1.1: The Kaikoura Peninsula on the East Coast of the South Island with the study sites shown and Edward Percival Field Station (E.P.F.S).

1.2.2 Specific Sites

(a)Sharks Tooth (Atia) Point (Plate 1.1)

This is the most exposed study site as it is on the tip of the Peninsula at the southern end. It is less exposed to northerly than to southerly seas but is strongly exposed to both southerly and easterly weather patterns. The substrate is argillaceous siltstone which is harder than the mudstone at the other two sites but not as rough as limestone. The point consists of a long, gently sloping platform of about 200m, that drops sharply into the subtidal. The point is isolated and windswept with an abundant algal flora in spring, winter and autumn but less so over summer.

(b) Wairepo Flats (Plate 1.2 & 1.3)

These are glauconite siltstone, better known as `mudstone', (Rasmussen, 1965) platforms on the northern side of the Peninsula, that extend up to one hundred meters from the high shore before dropping into the subtidal. It is a relatively sheltered site and is exposed only to north-easterly seas and consists of flat platforms with several raised areas. Most of these raised areas are bare of macroalgae year round. The predominant alga is *Hormosira banksii* on the low and mid shore, and the most abundant animals are *Melagraphia aethiops* (a gastropod mollusc) on the high shore and *Turbo smaragdus* on the low shore and various limpets.

(c)Mudstone Bay (Plate 1.4 & 1.5)

This bay has a southerly aspect and is located in the middle of the south side of the Peninsula. It is relatively sheltered due to the length of the bay. The outer edges are quite exposed and this is where the fieldwork done in this bay was carried out. Like Wairepo Flats, this bay consists of soft mudstone platforms that stretch up to fifty meters before they have a steep drop-off into the subtidal. There are many algal species within the bay and their abundance changes seasonally.

Plate 1.1: Sharks Tooth Point , general view of long sloping argillaceous siltstone platforms.

Plate 1.2: Wairepo Flats - general view showing mudstone platforms extending over 100m to the sea.

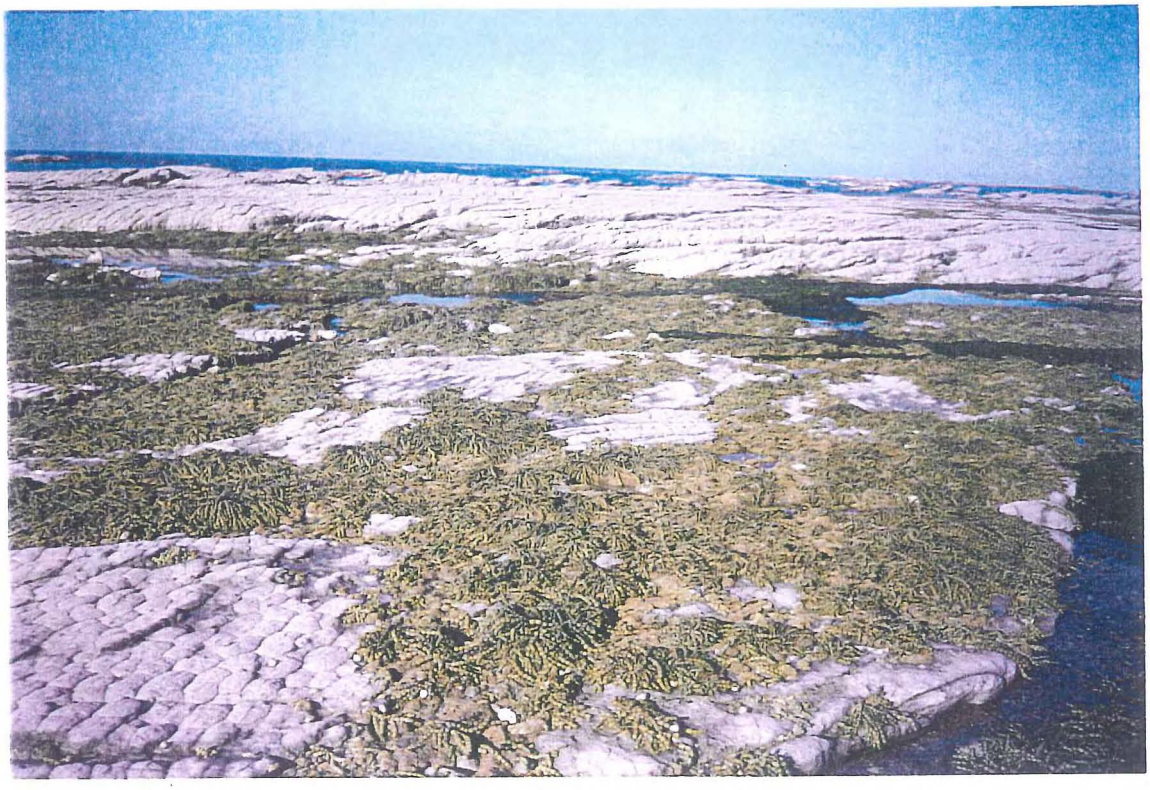


Plate 1.3: Wairepo Flats showing areas of *Hormosira banksii* interspersed with patches of bare rock.

Plate 1.4: Mudstone Bay in winter, at low tide, showing abundance of algae.

Plate 1.5: Mudstone Bay at low tide in summer, showing lack of algae.

1.3 Study Species

The most obvious feature of rocky shores is the zonation of plants and animals. The most apparent zones on rocky shores are the lower barnacle/mussel area and the higher algal zone. In New Zealand a typical rocky shore community consists of primary producers (fucoids and ephemeral algae such as *Ulva* sp, *Enteromorpha* and *Porphyra*), grazing herbivores (chitons, limpets and snails) and predatory carnivores (whelks, fish and birds).

Like all Siphonariids, *S.zelandica* are hermaphroditic (Quinn, 1988b) and unlike most gastropods have no operculum and no ctenidium (Walsby and Morton, 1982). Siphonariids have complex reproductive genitalia and development is direct from the egg. The eggs hatch into an operculate veliger that is free-living for a short period. The egg masses are encased in jelly, semicircular in shape and are found attached to the substrate in pools and damp crevices. The egg ribbons are generally yellow or white in colour and quite thick.

Walsby and Morton (1982) noted that *Siphonaria* are ecologically similar to archeogastropods except for a few important differences. These are a) the development of the shell `siphon', b) the mantle is closed entirely round the animal except for the pneumatosome (respiratory opening) and c) there are no head tentacles but the animals do have broad fleshy oral lappets.

The respiration of *Siphonaria* is very different from most gastropods and is well covered by Walsby and Morton (1982) and Wong (1980). When out of water, *Siphonaria* `breathe' with the mantle cavity, which acts as a lung while the pneumatosome is open. However, the mantle cavity fills when *Siphonaria* is submerged and a water current is created through the secondary, plicate gill (Figure 1.2).

Siphonaria zelandica is dull brown externally and often covered in algae with an irregular oval shell shape and distinct ribs. Internally the shell is cream with a brown band around the outer margin. Around Kaikoura it is found in large

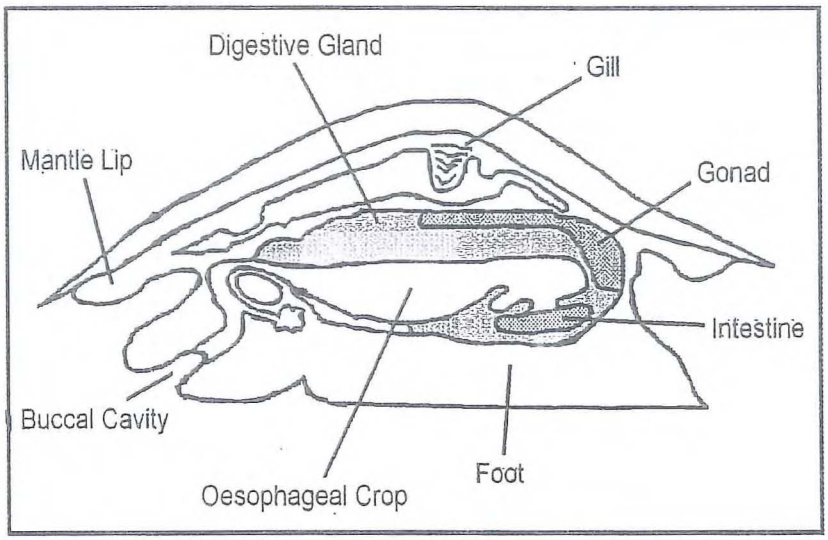


Figure 1.2: Diagram of *Siphonaria's* basic physiology (adapted from Walsby and Morton, 1982).

numbers on flat platforms consisting mainly of mudstone. They can be found occasionally on limestone. Whatever the substrate they are crack-orientated and are commonest in damp or wet areas (Plate 1.6). They can generally be found in the presence of encrusting algae or succulents such as *Enteromorpha*.

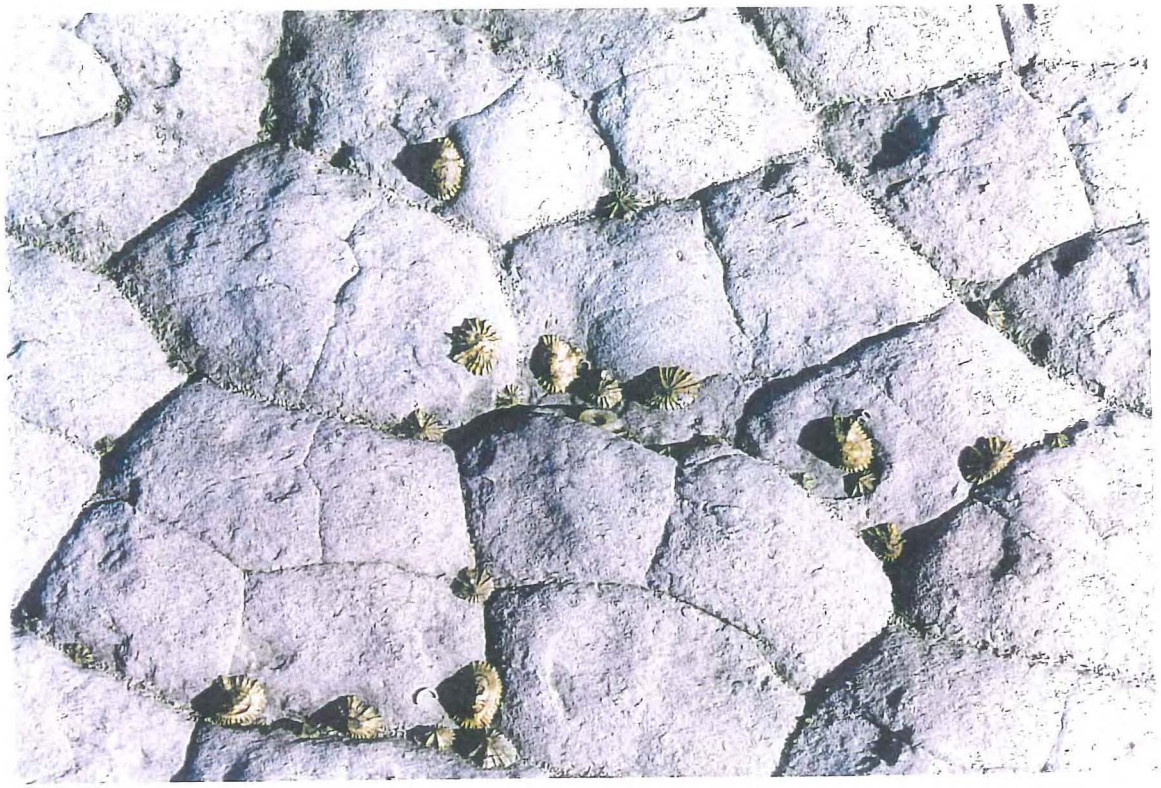


Plate 1.6: *S.zelandica in situ* on mudstone, showing preference for crevices.

1.4 Objectives

The specific aims of this thesis were to investigate the demography of *S.zelandica,* as its life history and reproductive processes have not been studied before. This meant looking at growth and mortality rates, distribution and abundance and reproduction. The reproductive study investigated timing and strength of spawning and overall fecundity. The experimental study concentrated on the ecology of *S.zelandica.* In particular, I tested the hypotheses that intraspecific competition affects the growth rates and mortality of *S.zelandica.* Also, the hypotheses that increased densities of *S.zelandica* will affect algal abundance was tested at two sites to compare exposed and sheltered shores. A second experiment tested the effects of a predacious whelk on *S.zelandica's* survival at both low and mid shore. Secondly, these same effects were investigated for bird predation (oystercatchers) on *S.zelandica* on the intertidal platforms.

SECTION ONE

DEMOGRAPHY

CHAPTER TWO

Demography

DISTRIBUTION and DEMOGRAPHY

2.1 Introduction

Population structure and changes through time provide a context for understanding the processes affecting populations. The habitats occupied by a species and interspecific associations are important components of the way direct and indirect factors affect populations (Menge, 1995). These factors include juvenile settlement patterns (Creese 1980c, Menge 1991), larval recruitment (Menge, 1991), a range of biotic interactions, such as predation and competition (Black 1979, Underwood et al. 1983) and physical factors (Allanson 1959, Garrity 1984, Hobday 1995). Each of these may operate on varying spatial and temporal scales (Menge and Olson, 1991). Menge (1991) developed the idea of direct and indirect interactions further, proposing four reasons for differences in distribution and abundance. They are: a) recruitment is not the only factor structuring a population, b) two or more factors may structure a population including indirect factors, c) variations in recruit numbers may be affected by variation in predation and competition and d) how abundance is measured may affect analysis. Patterns of size distribution of molluscs are generally believed to be due to migration of specific sizes in and out of an area to optimise food availability and decrease competition, and in response to different sized animals having different physical tolerances (Black 1979, Underwood et al. 1983, Hobday 1995).

In New Zealand there have not been many descriptions of mollusc species distribution in rocky habitats (see Creese, 1988). The first published information on the distribution of *Siphonaria zelandica* is in Batham (1956) which stated that *S.zelandica* is patchily abundant in overhung crevices. The only other study to have investigated the abundance of *S.zelandica* was done by Jeffs (1985). He found that populations in north-eastern New Zealand of *S.zelandica* occurred only on patches of its food source, *Ralfsia verrucosa*, and that intraspecific interactions controlled abundance.

To analyse the structure of a population or community, information in particular on the growth and mortality of the organisms within it is vital. There are three main recognised methods of measuring growth of individuals within a mollusc population (Creese, 1981): a) sampling a population over time and calculating the mean size of individuals in distinct age cohorts from polymodal size-frequency distributions, b) using growth checks on a shell or c) mark/recapture methods. Problems with these methods have been examined (Francis, 1988) but mark/recapture is generally considered to be the most reliable method for measuring individual growth and variation. As with any form of measurement there can be inaccuracies, such as errors in measurement at time of tagging or at recapture (Francis, 1988) or the loss of tags and how to estimate this loss (Treble et al. 1993).

Growth rates, as in many other organisms, vary within and between species of limpets. Suggestions for the cause of such variation include height on the shore (Sutherland 1970 & 1972, Creese 1980c, Hobday 1995), food availability/limitation (Underwood and Creese 1976, Creese 1981, Ortega 1985), density effects (Creese and Underwood 1982, Quinn 1988a, Menge 1991, Petratis 1992) or energy requirements (Tablado et al. 1994). There have been several studies on growth and mortality in species of *Siphonaria*. Most of them agree that tagging is a better measure of growth than size frequency distributions as trying to distinguish cohorts from size frequency data can be virtually impossible (Creese 1981, Creese 1988, Quinn 1988a). There are also problems with mark/recapture methods in *Siphonaria* species as it is difficult to tag limpets smaller than ten millimetres (Creese, 1988). Therefore, in *Siphonaria* species, it is not practical to estimate age from size (Tablado et al. 1994) and it is better to use methods independent of size to establish growth (Creese, 1988). In the only study on *S.zelandica*, Jeffs (1985) found growth to be extremely variable, dependent on population density and position of the limpets on the shore.

Mortality can also be assessed using the tagging method provided that tag loss is not confused with mortality. Migration must also be considered when an individual disappears from the population (Fletcher, 1984a) although in homing species this should be less of a problem. In my study, two methods of measurement were used to assess the growth and mortality of *Siphonaria zelandica* at two sites.

Understanding of reproductive processes aids in understanding an organisms demography. Time of spawning, amount of reproductive effort and the methods used to produce offspring determine the periodicity and intensity of larval production. Reproduction in limpets has been studied and reviewed by many researchers such as Korringa 1947, Sutherland 1970, Gonor 1972, Balaparameswara Rao 1973 & 1975, Grange 1976, Tompa 1979, Underwood 1979, Creese 1980b, Creese 1981, Creese and Ballantine 1983, Fletcher 1984b, and *Siphonaria* species outside of New Zealand have been reasonably well documented (Cottrell 1910, Allanson 1959, Mapstone 1978, Creese 1980a, Quinn 1988b). Limpets with a short breeding season are relatively easy to investigate while those with a long season or those that spawn continuously are much more difficult (Creese and Ballantine, 1983). Several key methods can be used for determining patterns of reproduction. Subjective gonad indices divide the reproductive condition into five stages and are a visual measure of condition (Balaparameswara Rao 1973, Creese and Ballantine 1983). A gravimetric gonad index is often used to elucidate the reproductive cycle (Creese and Ballantine, 1983). A gonad index generally involves a measure of gonad size or weight in relation to animal body size or weight, which removes the effect of individual size from the estimate of relative gonad quantity (Gonor, 1972). The gravimetric gonad index is normally expressed as a percentage and used to determine patterns of spawning and resting (Choat and Black, 1979) although one inherent assumption is that a decrease in the index indicates a spawning occurrence (Giese, 1959). Gonad indices are normally interpreted in conjunction with histological studies to determine the reproductive stages of a species (Gonor, 1972) and it is generally accepted

that using more than one method of measurement will give a more accurate assessment of the reproductive condition (Creese and Ballantine, 1983). Reproductive cycles can be affected by several parameters - size of adults (Creese, 1980b), food supply (Sutherland 1970, Fletcher 1984b), temperature (Grange, 1976) and water stress (Fletcher, 1984). In many species it is believed that a specific spawning stimulus is needed to induce spawning, such as wave splash/wetting (Grange 1976, Creese 1980b, Fletcher 1984a).

Although the reproductive process of *S.zelandica* has not been studied, much is known about *Siphonaria* species in general. Most *Siphonaria* species are hermaphrodites and many are believed to produce eggs and sperm simultaneously. Their reproductive system is complicated, with their organs being quite large compared to body size (Cottrell, 1910). The basic structure of the reproductive system of *Siphonaria* incorporates a hermaphrodite gland linked to a common duct which runs into the penis and the genital pore (Figure 2.1).

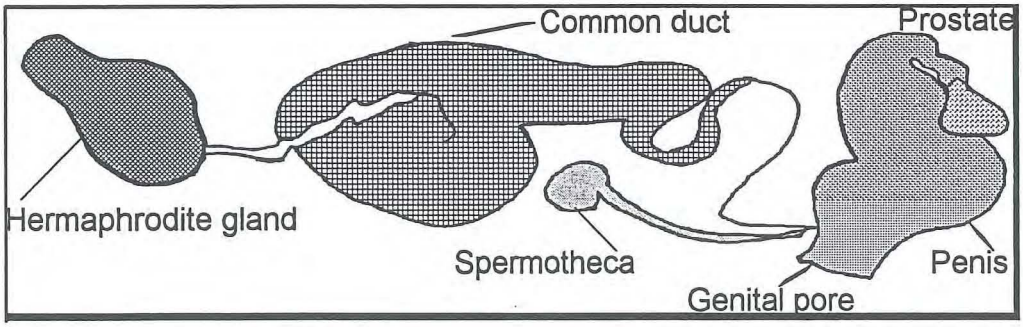


Figure 2.1: Basic diagram of the reproductive system of *Siphonaria* species (after Cottrell, 1910).

The hermaphrodite gland is the main reproductive organ and is clearly visible when the shell is removed from the limpet's body as it is orange in colour and is partially embedded in the brown digestive gland at the posterior end of the animal. The hermaphrodite gland is where the ova and sperm originate. Within the gland there are inner and outer follicles; the outer follicles are where the ova develop while spermatozoa arise within the inner follicles (Cottrell, 1910). At maturity the gametes pass into the common duct system, are

fertilised eggs are deposited in a gelatinous ribbon which becomes attached to the substrate (Plate 2.1). Eggs within this semicircular ribbon are in individual gel capsules and are connected to each other by threads (Mapstone, 1978). The colour of the egg ribbons varies with the stage of their development and, in general, planktotrophic veligers hatch a week or so after being spawned (Mapstone 1978, Creese 1980a). Some *Siphonaria* species have direct development, with no veliger stage, (Creese, 1980a) but this seems to be the exception rather than the rule.

Plate 2.1: Gelatinous egg masses of *S.zealandica in situ* at Wairepo Flats, Kaikoura.

Most *Siphonaria* species in Australia and South Africa have an extended breeding season (Creese 1980a, Quinn 1988b), there is normally a time lag of a month or two between spawning and when juveniles can be seen on the shore. Fecundity in *Siphonaria* species can be extremely variable and has been found to increase with increasing adult size (Creese, 1980a) and to be closely linked to food availability (Quinn, 1988b). As there have been no studies on reproduction in *S.zelandica*, the aim of this work was to examine

gonad development, reproductive cycle, time of spawning, fecundity of adults and the length of the embryonic stage.

2.2 Materials and Methods

Distribution and Abundance

Spatial and Temporal Sampling

At Wairepo, Sharks Tooth and Mudstone Bay permanent transects were run from low water to the high water mark. Three transects were run at each site and the ends were marked by a weatherproof flexible plastic strip nailed to the substrate. Transects were sampled on days of calm water and low tides (0.1 or 0.2m). Every five meters along each transect, three random 0.25m^2 quadrats in a corridor of 10m around the tape were sampled counting all animal species present. Also the percentage cover of each algal species present was identified and visually estimated using a grided quadrat. This sampling was done quarterly from January 1995 to December 1995 to examine the temporal structure of the shore.

Growth and Mortality

Size Frequency

At all three sites five randomly selected `patches' (areas of slightly raised rock) were permanently marked with plumbers' tape in October 1994. Every month from October 1994 to December 1995 these patches were sampled using three random 0.25m^2 quadrats in each patch. All *Siphonaria* in each quadrat were counted and their length measured to the nearest 0.02mm using Vernier callipers.

Mark/Recapture Methods

At the Wairepo Flats and Sharks Tooth sites, two hundred limpets were number-tagged, by supergluing (Selly's Supaglue™) a vinyl tag 5mm long onto each shell. Once a tag was bonded to a shell, a thin layer of five-minute Araldite™ was applied over the top of the tag to make it more secure. Limpets

over a wide size range, 4mm - 26mm, were tagged and their length measured to the nearest 0.02mm. Tagged limpets were remeasured monthly.

Reproduction

Gonad Index

Each month from October 1994 to February 1996, thirty limpets between 14-19mm were collected from Wairepo using a flat bladed knife. This is the most common size range, as determined from size frequency data, and few limpets grow larger than 25mm. By selecting limpets in a restricted size range variation in both the gonad and body weight are virtually eliminated.

In the laboratory, all algae adhering to the shell was removed and shell length was measured to the nearest 0.05mm. The whole animal, shell included, was then weighed on a Mettler balance to the nearest 0.001g. The body of the animal was dissected out from its shell by cutting the horseshoe-shaped attachment muscle. The shell and animal were weighed separately. The animal was preserved in Bouin's fixative for one month before being reweighed, then the gonads were dissected out and weighed separately.

Gonad Histology

The gonads dissected out for determination of the gonad index were stored in 70% ethanol before being transferred into plastic cassettes and processed in a Shandon Citadel 1000 embedding machine (for method see Appendix A). Once embedded the gonad was floated off into wax moulds which were left overnight to harden. Sections 7 microns thick were then cut from the embedded material using a rotary microtome and steel knife. These sections were placed on glass slides with Haupt's adhesive, dried in a 30°C oven for 12 hours before being stained with Ehrlich's haematoxylin and eosin in a Shandon Varistain 24-4 machine (for procedure, Appendix A). Once stained, glass coverslips were mounted on the slides using Eukitt resin.

The sections were then examined to assess gonad composition. Five sections on each slide were studied under a binocular microscope with a grid mounted in the eyepiece. Twenty intersections on the grid were randomly selected and the type of material beneath each was recorded. Mean percentage mature and immature oocytes and sperm material were calculated and plotted against sampling month. Several sections of tissue of animals collected at different time periods were then selected and colour photographs taken using an Olympus BH2 compound microscope and camera system. This was to show what the hermaphrodite gland looked like over the breeding period.

Hatching and Settlement

Egg masses were removed from the substrate at Sharks Tooth and taken back to the lab. Here they were placed in constantly aerated seawater in glass containers until they hatched. The water was changed slowly each day to resemble the drying/submersion cycle of the daily tides. Once the eggs had hatched several plates of different types of substrate (limestone, mudstone, and greywacke) were placed in plastic tanks and covered with water. The hatched veligers were added to the containers with the settlement plates and observed to see if there were any substrate preferences.

Fecundity

Two methods of determining fecundity were used. Antifouling paint was used to enclose five squares of 0.25m^2 on the rocks at the Wairepo site in October just before *Siphonaria* were next expected to spawn. The number of limpets present in each quadrat was noted and they were paint marked and their length measured. Egg masses were counted daily in each quadrat. Egg masses were then carefully removed from the substrate and taken back to the laboratory.. Three small portions were cut from the ribbon, weighed and examined under a binocular microscope to count the number of eggs (Creese, 1980a). The data from this study was used to estimate the number of eggs per egg mass. The second method of measuring fecundity involved collecting a broad size range of *S.zelandica* pre-during and post-spawning. These limpets were removed

their shell, weighed and fixed in Bouin's for a week prior to the gonad being dissected, weighed and the eggs teased out under a compound microscope and counted.

2.3 Results

Distribution and Abundance

Spatial Sampling

The transects at Wairepo Flats were long and gently sloping with no major topographic changes. There were many different species present on the shore so only those important to this study are presented. Percent algal cover at Wairepo Flats was highest on the low shore (over 40%) (Figure 2.2a) but dropped in the lower mid shore region (35m) before showing another increase at 45m up the shore. There was no algal cover on the high shore, above 70m. *S.zelandica* was abundant within a 30m area of the upper low and lower mid shore. *Turbo smaragdus,* cats-eye, was most abundant in the same area as *S.zelandica*. At Wairepo Flats the only other species with significant numbers at any level of the shore was *Melagraphia aethiops* which were greatest on the high shore.

Mudstone Bay platforms were short and exposed to a high level of wave splash. Percent algal cover remains quite high, greater than 40%, up until the high shore where it drops to zero (Figure 2.2b). The decrease in percent cover up the shore is gradual. The gastropod species composition is quite different at Mudstone Bay in comparison to Wairepo Flats. In particular, although *S.zelandica* was most abundant over the mid shore region it did occur quite high up the shore. Again *M.aethiops* was the most abundant animal species on the high shore although it was present on the low shore as well. *Cellana* spp. were abundant on the low shore and in areas of the upper mid to high shore. Whelks and *T.smaragdus* were abundant on the low shore but were not present in other areas at this site.

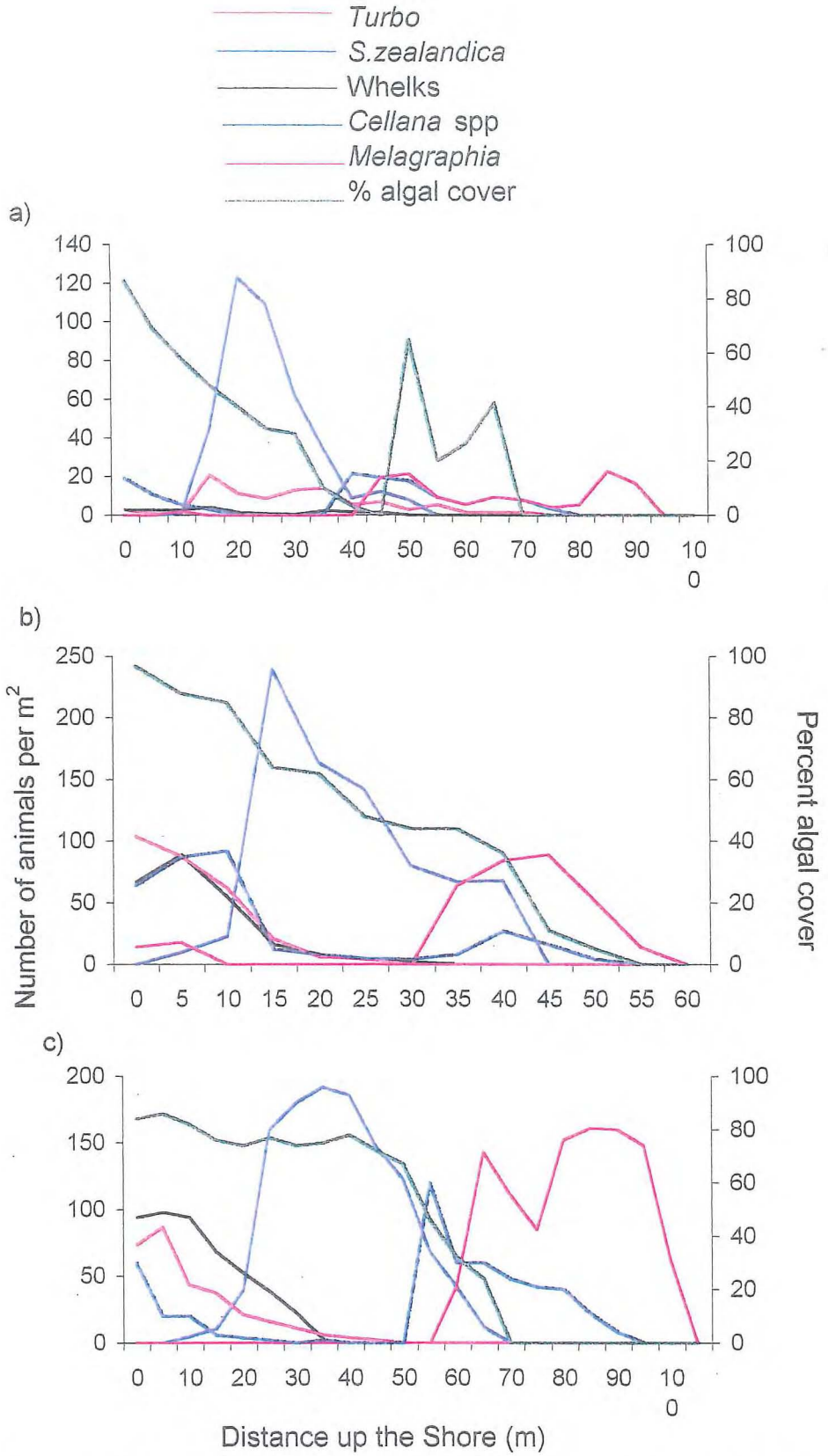


Figure 2.2: Percent algal cover and numbers of *Turbo smaragdus*, *S.zelandica, Melagraphia aethiops*, whelks and *Cellana* species pooled from three transects at **a)** Wairepo Flats, **b)** Mudstone Bay and **c)** Sharks Tooth Point.

60%, but it dropped in the upper mid to 30% cover and there were no algae in the high shore (Figure 2.2c). The gastropod species distribution is quite different to the other two sites. *S.zelandica* occurred mainly in the mid shore region but not in the high shore. *Cellana* spp were abundant low on the shore yet were present in the mid and high shore. *M.aethiops* was abundant at the high shore and upper mid but is not present on the low shore. Whelks and *T.smaragdus* were present low on the shore like the two other sites but in quite high numbers. All species occurred in greater numbers at Sharks Tooth than they did at the other sites.

Temporal Sampling

Percentage algal cover over time at all three sites showed similar trends (Figure 2.3). At all sites the low shore had the most algal cover regardless of time of year, then the mid shore had the next greatest amount and finally the high shore had the least amount of algal cover. At Sharks Tooth and Wairepo the high shore had sparse algal cover during most of the year while at Mudstone there was 10% algal cover at high shore in winter (June) and 5% in spring (September). The low and mid shore had similar levels of algal cover in March, June and September at Sharks Tooth but the mid shore droped to 20% in summer and although there is a drop at the low shore, there is still 55% cover here in summer.

Mudstone Bay at both low and mid shore were also similar in June and September but the mid shore had markedly less algae in March and December, less than 40%, than the low shore. The low shore stayed quite high with 70% or greater algal cover. Wairepo Flats had less algal cover at the mid shore over time, up to 60%, than at the low shore which never had less than 60% cover.

The number of *S.zelandica* at each site varied over time but Wairepo always had the least numbers overall while Mudstone Bay always had the most. Mudstone never had less than 110 limpets/m^2 (+/-0.068) while both Sharks

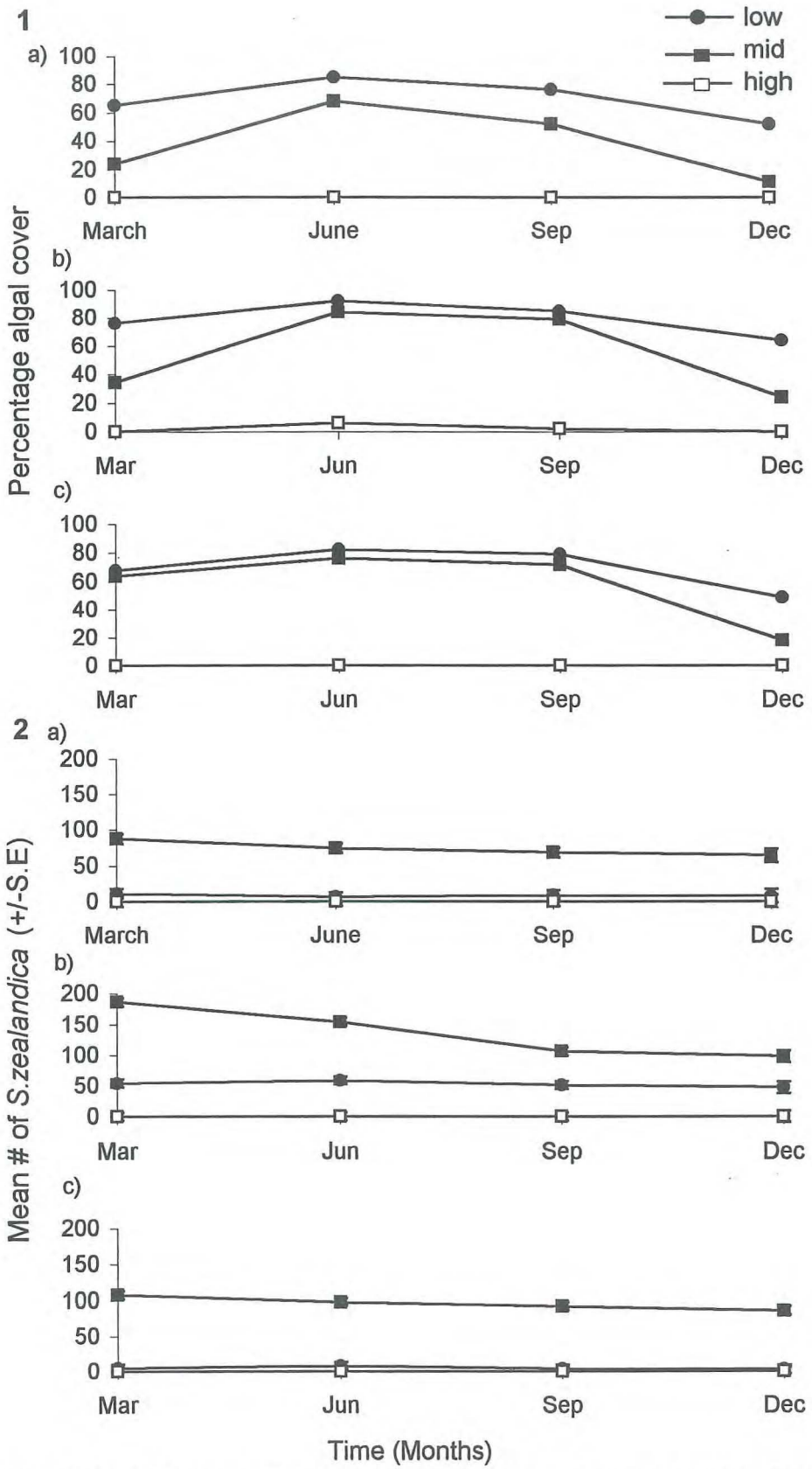


Figure 2.3: **1)** Percent algal cover and **2)** number of *S.zelandica* in transects at **a)** Wairepo Flats, **b)** Mudstone Bay and **c)** Sharks Tooth Point over time.

S.zelandica at any time of the year at the high shore level and at Wairepo and Sharks Tooth there were few limpets in the low shore, less than 10/m^2 (+/-1.6). However at Mudstone there were consistently 50 limpets/m^2 (+/-0.69) at the low shore. Mid shore was where *S.zelandica* was most abundant and this is the same for all three sites.

The overall associations between *S.zelandica* and the other intertidal species is illustrated for each site in Table 2.1. *S.zelandica* was negatively correlated with *M.aethiops* and *Cellana* species at Wairepo Flats but is positively correlated with percent algal cover. At Mudstone and Wairepo *S.zelandica* is again correlated with algal cover but also with *Cellana* species. The other species that were measured were negatively correlated with *S.zelandica*.

Table 2.1: Correlation matrix for *S.zelandica* at all three sites with percent algal cover and other intertidal gastropods. Significant values ($p<0.05$) for *S.zelandica* are in bold.

Wairepo Flats	% algal cover	*S.zelandica*	Whelks	*T.smaragdus*	*M.aethiops*
S.zelandica	**0.157**				
Whelks	0.558	**0.179**			
T.smaragdus	0.171	0.665	0.527		
M.aethiops	-0.209	-0.346	-0.437	-0.316	
Cellana species	0.353	-0.329	0.239	-0.099	0.230
Mudstone Bay	**% algal cover**	***S.zelandica***	**Whelks**	***T.smaragdus***	***M.aethiops***
S.zelandica	**0.267**				
Whelks	0.801	-0.233			
T.smaragdus	0.808	-0.245	0.971		
M.aethiops	-0.364	-0.324	-0.292	-0.283	
Cellana species	0.757	**0.303**	0.922	0.887	-0.114
Sharks Tooth	**% algal cover**	***S.zelandica***	**Whelks**	***T.smaragdus***	***M.aethiops***
S.zelandica	0.570				
Whelks	0.643	-0.202			
T.smaragdus	0.606	-0.202	0.947		
M.aethiops	-0.812	-0.523	-0.461	-0.425	
Cellana species	-0.158	0.309	-0.032	0.020	0.141

Growth and Mortality

Size Frequency

At Sharks Tooth Point (Figure 2.4) cohorts are hard to distinguish and they tend to coalesce around 10mm. Arrows point to one possible cohort moving through time. Recruitment appears to occur in February/March and November/December. There are few large limpets at this site, that is larger than 20mm, and they can be seen to disappear over time. The bulk of the limpets at this site are in the 10-18mm size range. Wairepo Flats has less limpets than at Sharks Tooth (Figure 2.5). There are more large limpets than at Sharks Tooth but they are still not abundant. Again arrows show a possible cohort moving through time. Recruitment is slightly later at this site than at Sharks Tooth, occurring in April/May (early winter). Mudstone Bay id quite different to the other two sites (Figure 2.6). There are more *S.zelandica* at this site than at Wairepo but less than there are at Sharks Tooth. There are very few small limpets and lots of larger limpets. It is difficult to work out any cohorts and the limpets tend to recruit in March/April (autumn).

Mark/Recapture

Growth at both Wairepo Flats and Sharks Tooth Point of tagged S.zelandica showed that overall the two sites are similar (Figure 2.7). At Wairepo, S.zelandica put more weight on at smaller size classes than at Sharks Tooth. When this is broken into size classes within seasons, covariance analysis showed that Wairepo grew more in winter in all size classes but in the other seasons the two smaller size classes are similar between sites (Figure 2.8). Sharks Tooth had a significant difference in all size classes in all seasons. Overall there was a significant difference between sites ($p=0.000$), cohorts ($p=0.000$) and seasons ($p=0.000$) (Table 2.2). Seasonal differences at Wairepo are that there is less growth in summer than in other seasons. At Sharks Tooth growth is again less in summer but it is more consistent over the seasons. Bi-monthly growth for both sites in all seasons shows much variance between months (Figure 2.9 &2.10, for size breakdown see Appendix B).

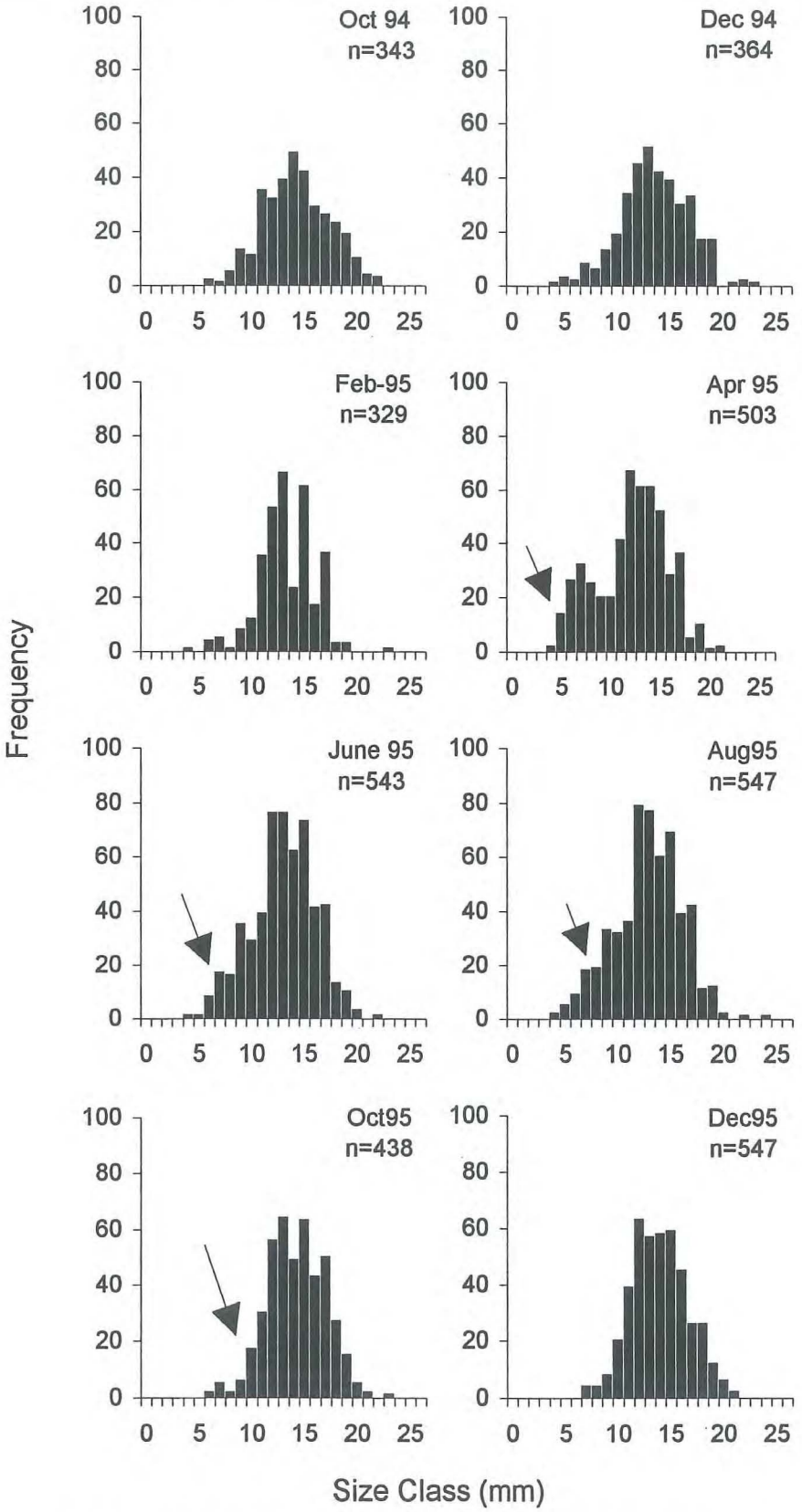


Figure 2.4: Bi-monthly size frequency distributions of *S.zelandica* at Sharks Tooth Point from October 1994 to December 1995. Arrows point to possible cohorts.

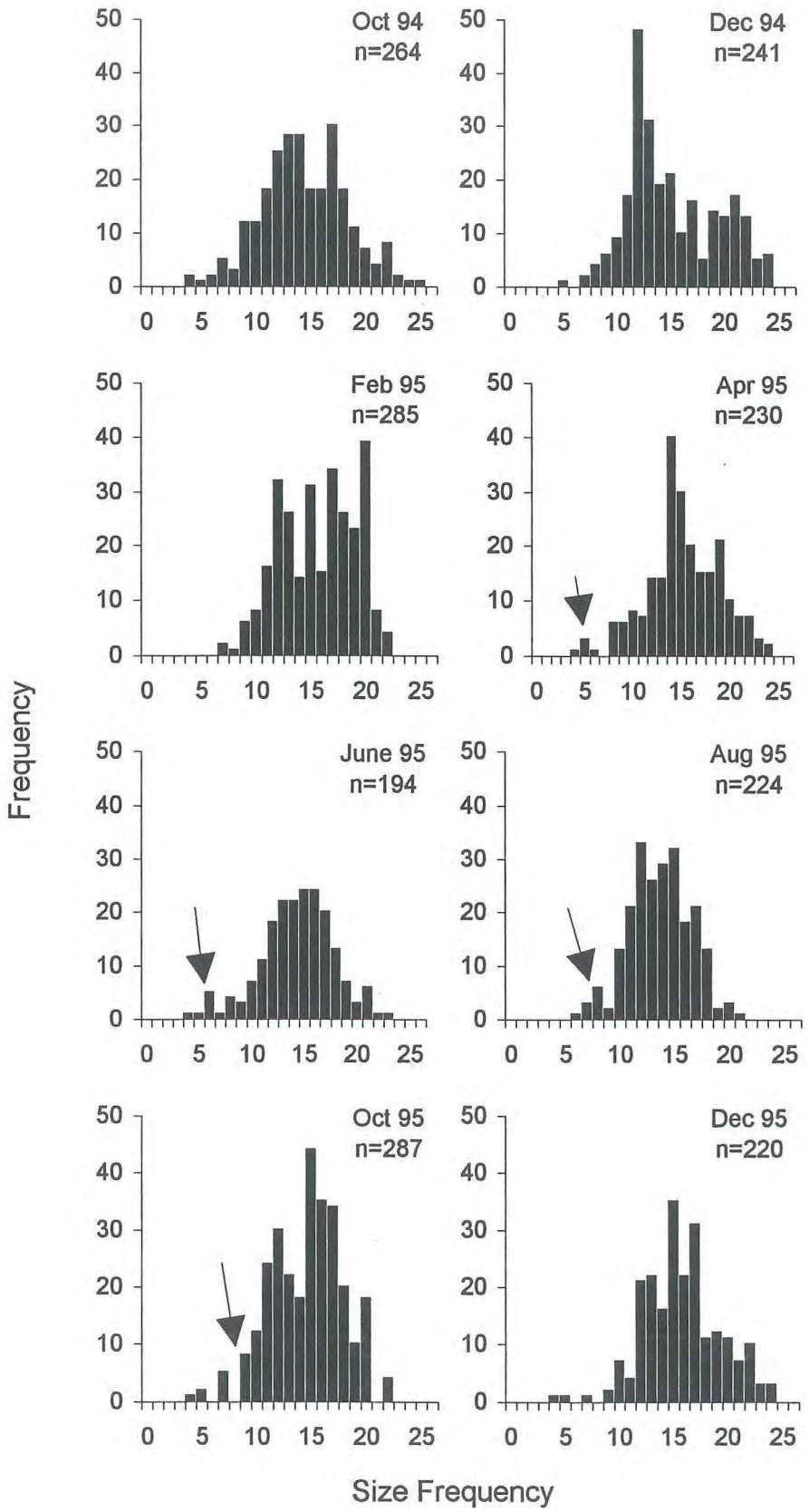


Figure 2.5: Bi-monthly size frequency of *S.zelandica* at Wairepo Flats from October 1994 to December 1995. Arrows point to possible cohort.

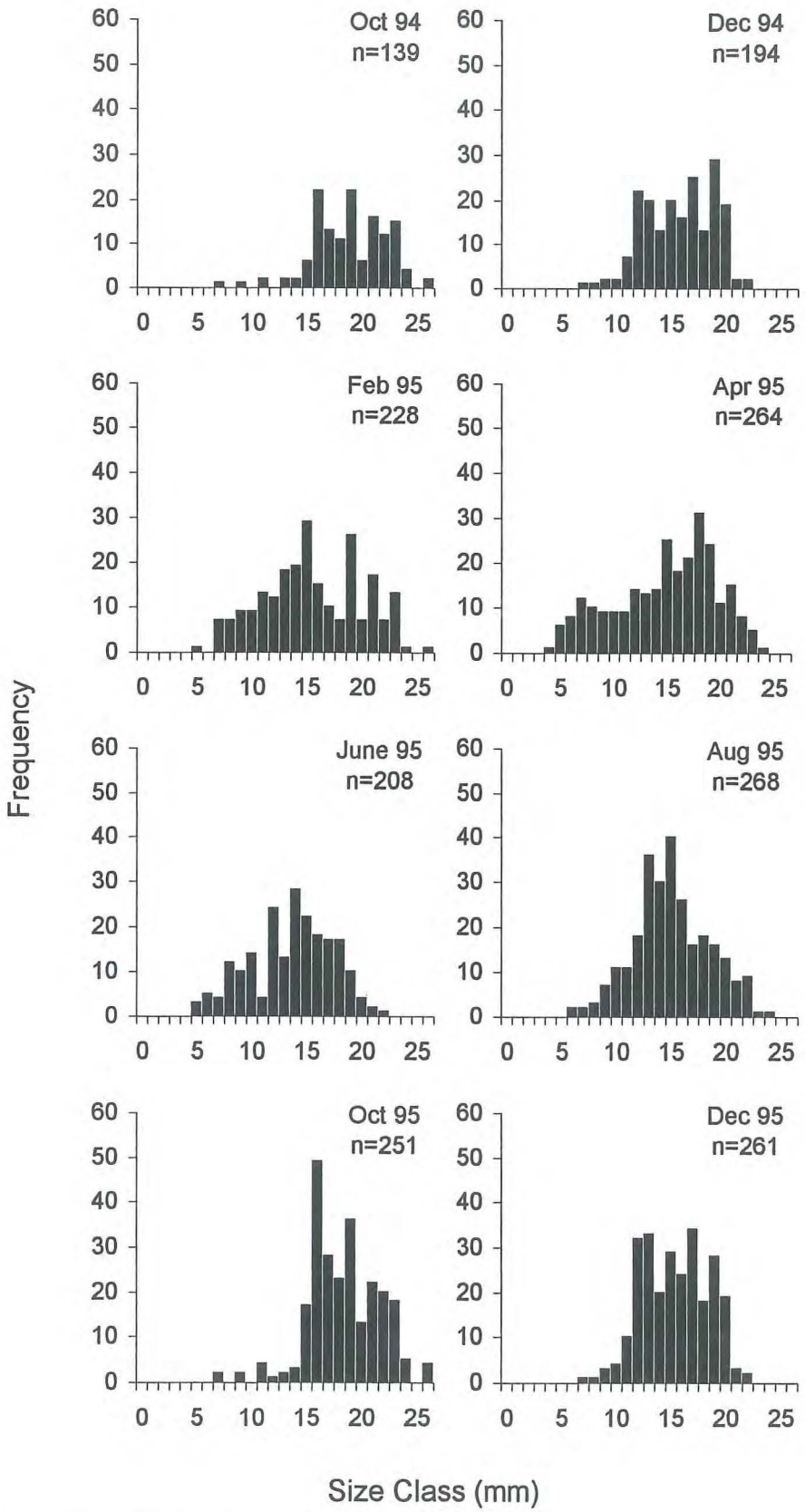


Figure 2.6: Bi-monthly size frequency distributions of *S.zelandica* at Mudstone Bay from October 1994 to December 1995.

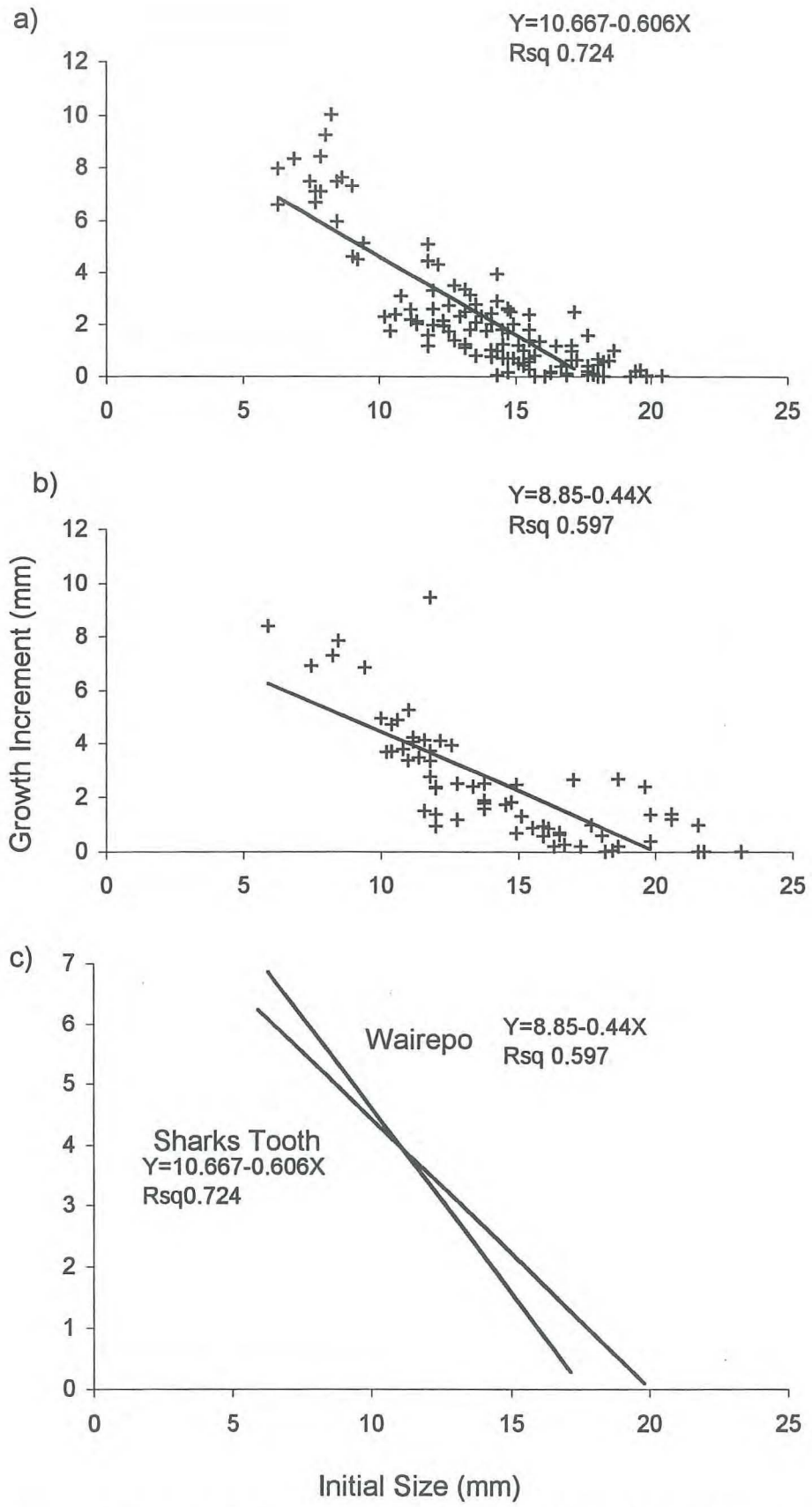


Figure 2.7: Growth for tagged *S.zelandica* from **a)** Sharks Tooth Point, **b)** Wairepo Flats and **c)** regression lines for both sites for the year February 1995 to February 1996.

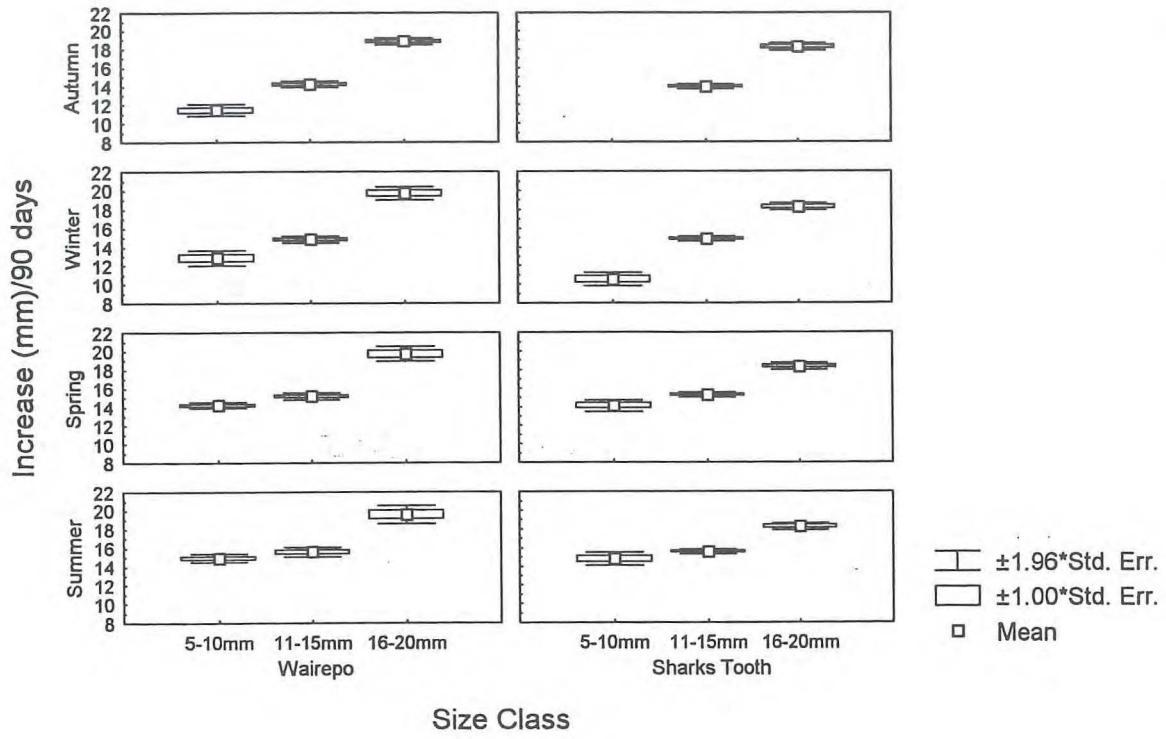


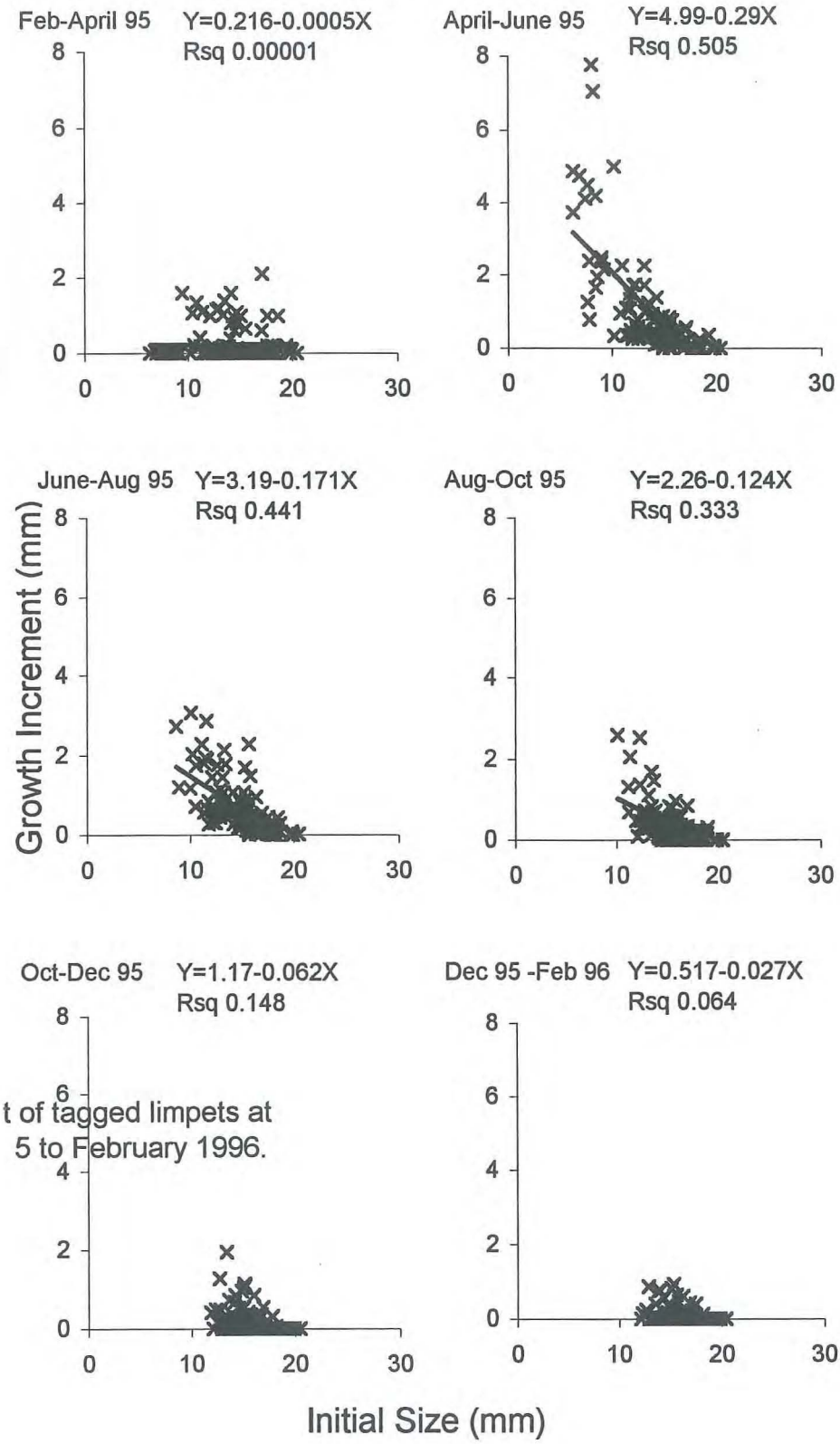
Figure 2.8: Box and whisker plots for growth increase over 90 days for three size classes at Sharks Tooth Point and Wairepo Flats in four seasons.

Table 2.2: Main Covariance results showing significant differences. Variances homogenous, (Cochrans test p>0.05)

Source	df	MS	SS	F	p
Site	1	138	138	18.71	0.000
Cohort	2	2284	4568	786.6	0.000
Season	3	44	132	5.94	0.000

Growth curves for the different size classes taken from the tagged *S.zelandica* data (Figure 2.11) that larger size limpets have very little growth over time while the smaller limpets grow quite quickly for the initial few months after they have settled before slowing their growth.

Mortality at Sharks Tooth and Wairepo is quite different but this is largely due to a storm at Wairepo (Figure 2.12). If the storm event had not occurred then survival at the two sites would have been very similar. At both sites the larger



t of tagged limpets at
5 to February 1996.

Figure 2.9: Bi-monthly growth increment of tagged limpets at Sharks Tooth Point from February 1995 to February 1996.

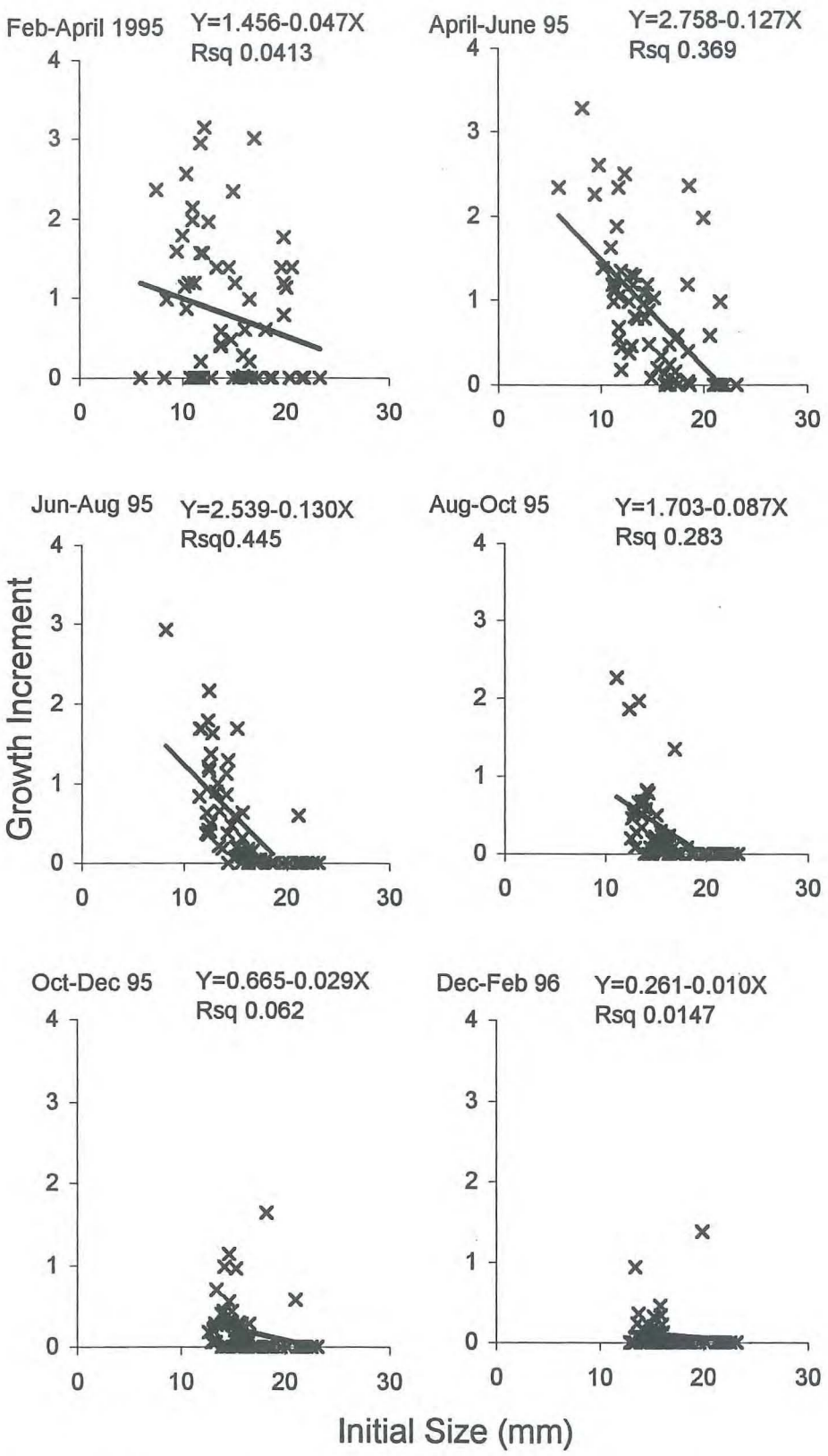


Figure 2.10: Bi-monthly growth increment of tagged limpets at Wairepo Flats from February 1995 to February 1996.

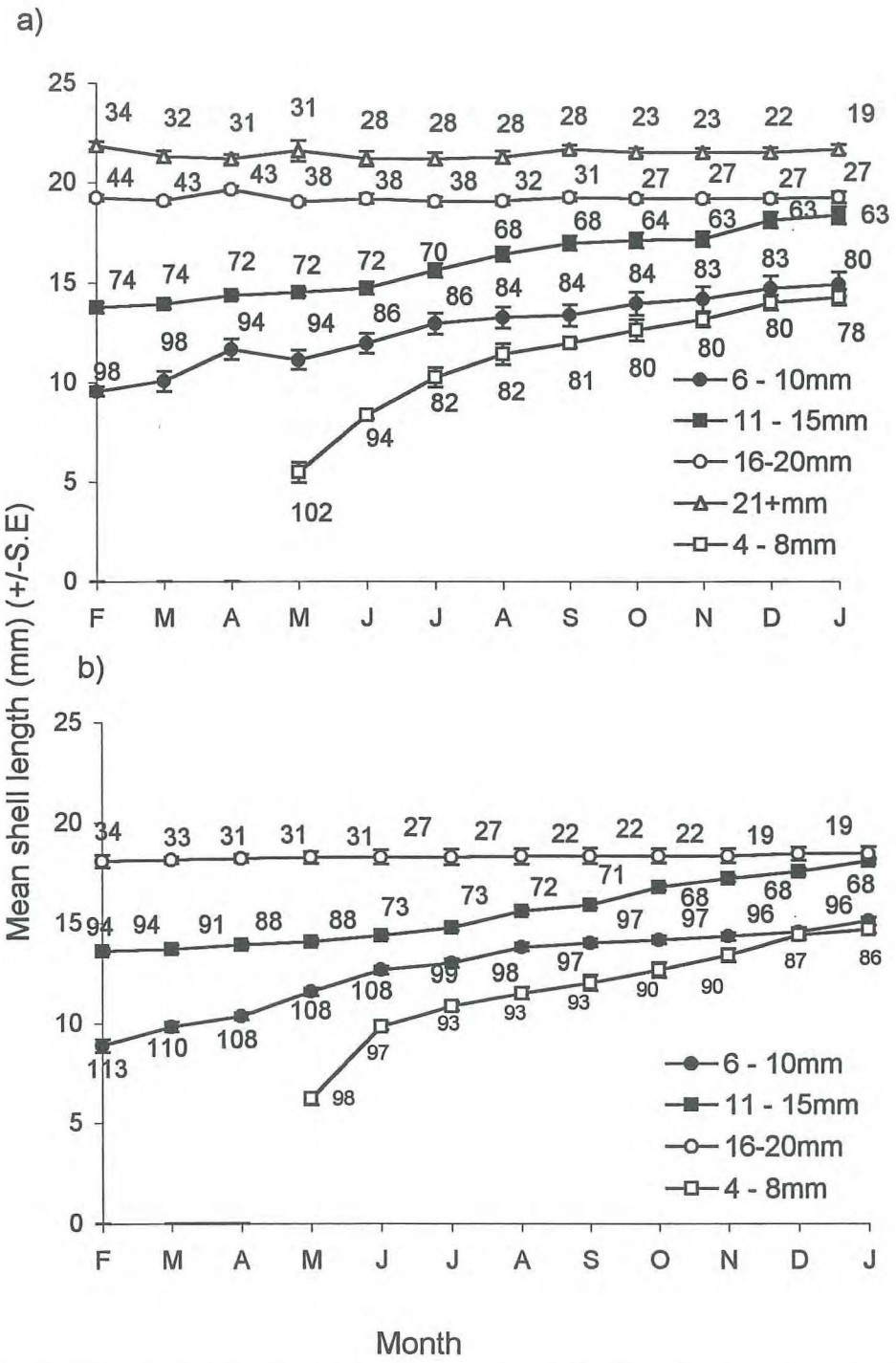


Figure 2.11: Mean growth per month of *S.zelandica* for different size ranges at a) Sharks Tooth and b) Wairepo Flats from February 1995 to January 1996. Data labels are number sampled each month (surviving limpets).

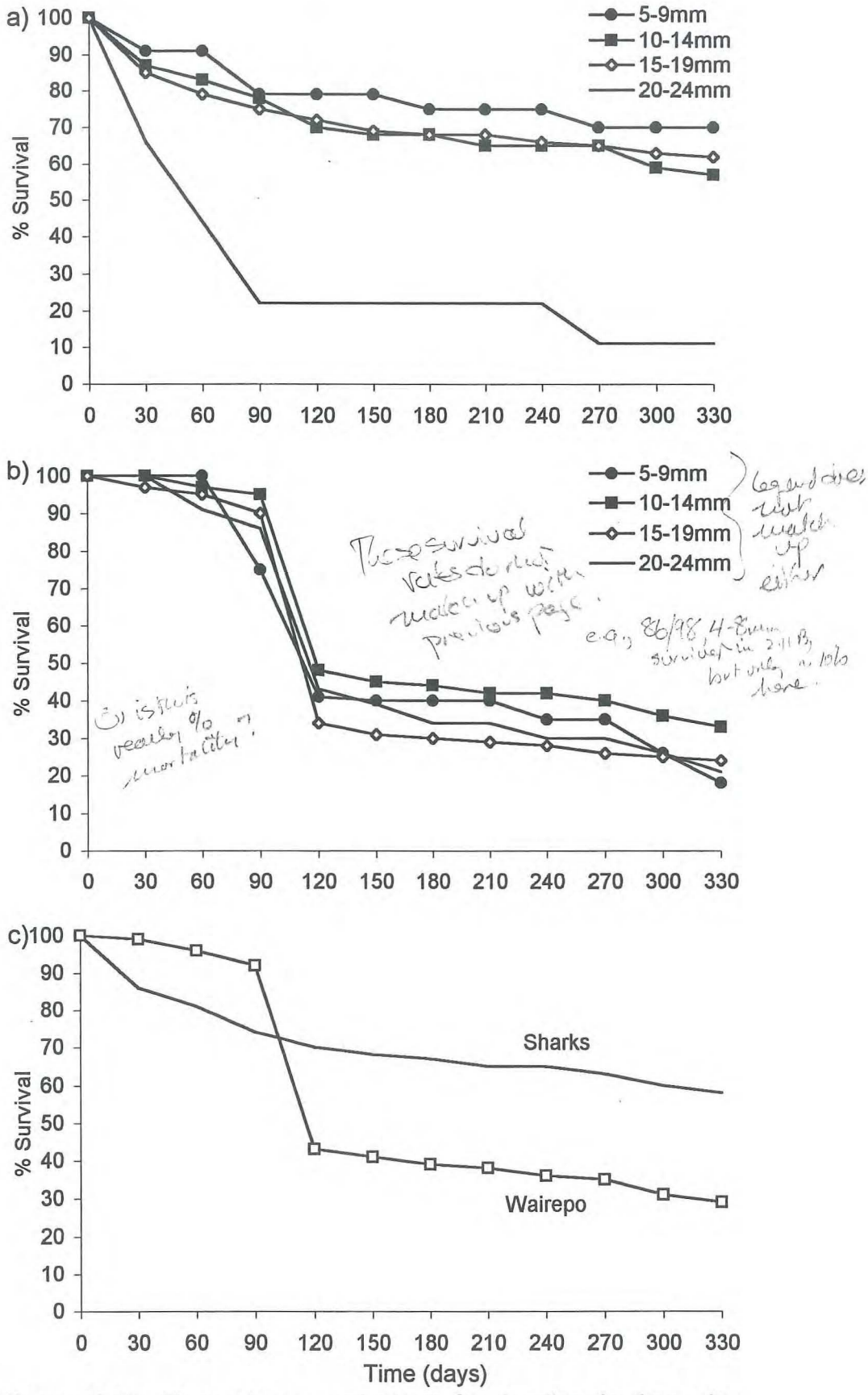


Figure 2.12: Percentage survival of *S.zelandica* in four size ranges over time at **a)** Sharks Tooth, **b)** Wairepo Flats and **c)** overall survival at both sites.

size classes, from 15 - 25mm, have the worst survival while the smallest size classes, 5 - 9mm, have the best.

Reproduction

Gonad Index

The gonad index (Figure 2.13) shows a peak in January/February of both 1995 and 1996 and also a peak in September/October of 1995. It appears that there was also a peak in September/October 1994 as when measurements were started in October 1994 the index was high. These peaks are indicative of spawning events and the throughs that follow them indicate resting phases. An ANOVA done on the three peaks showed a significant difference (p=0.000) between them but not between years.

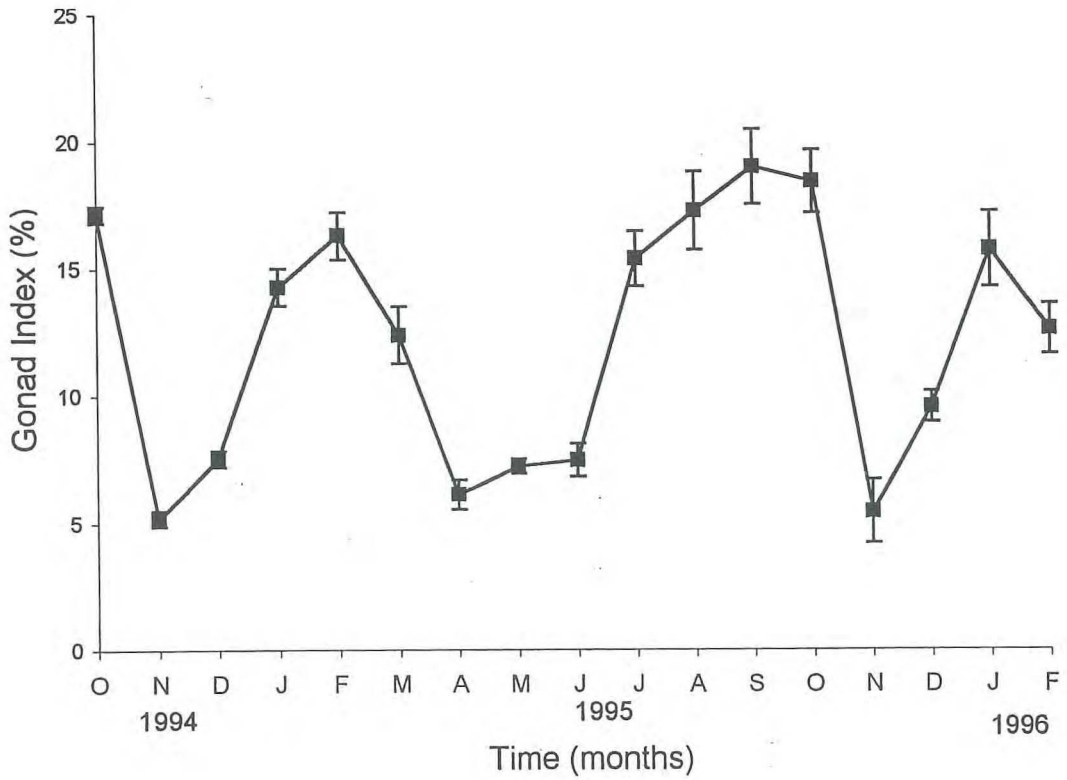


Figure 2.13: Mean Gonad Index %(+/-S.E) for *S.zelandica* from October 1994 to February 1996.

Gonad Histology

From the sections on the slides that were viewed, it was seen that there are 30% or more mature oocytes present in the gonad at all times. There are peaks of mature oocytes in February 1995 and 96 and in September of 1995.

At these peaks there is 80% or more mature oocytes (Figure 2.14). Immature oocytes are almost the mirror image of the mature oocytes, having troughs down to 5% in February and September. Immature oocytes never got higher than 50% of the gonad composition. The percentage of sperm material stayed fairly stable over the entire year with it fluctuating between 15 and 25%. There were no large peaks or troughs for the sperm material like there was for mature and immature oocytes.

Photos taken from the histological sections showed mature and immature oocytes at the outer edge of the gonad section while the sperm material was toward the centre (Plates 2.2, 2.3). There are mature oocytes right on the cell wall and immature oocytes are dark purple circles toward the middle of the section, near the sperm material (Plate 2.2). The thick black areas on Plate 2.4 are masses of heads of spermatozoa and plate 2.5 shows oocytes with their nucleus clearly visible.

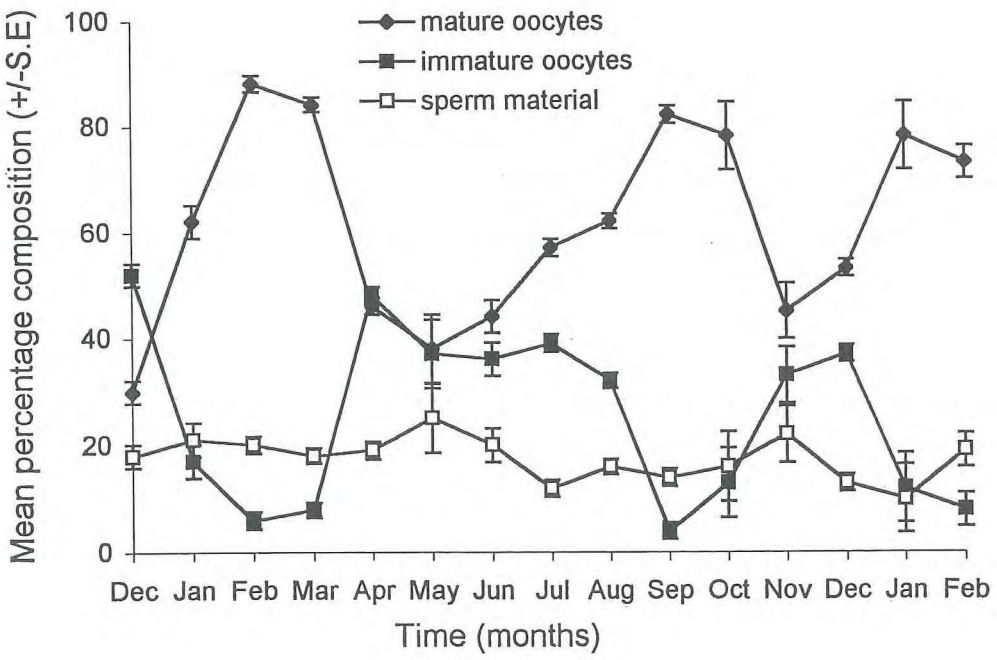


Figure 2.14: Percentage composition of *S.zelandica* gonads over time, December 1995 to February 1996.

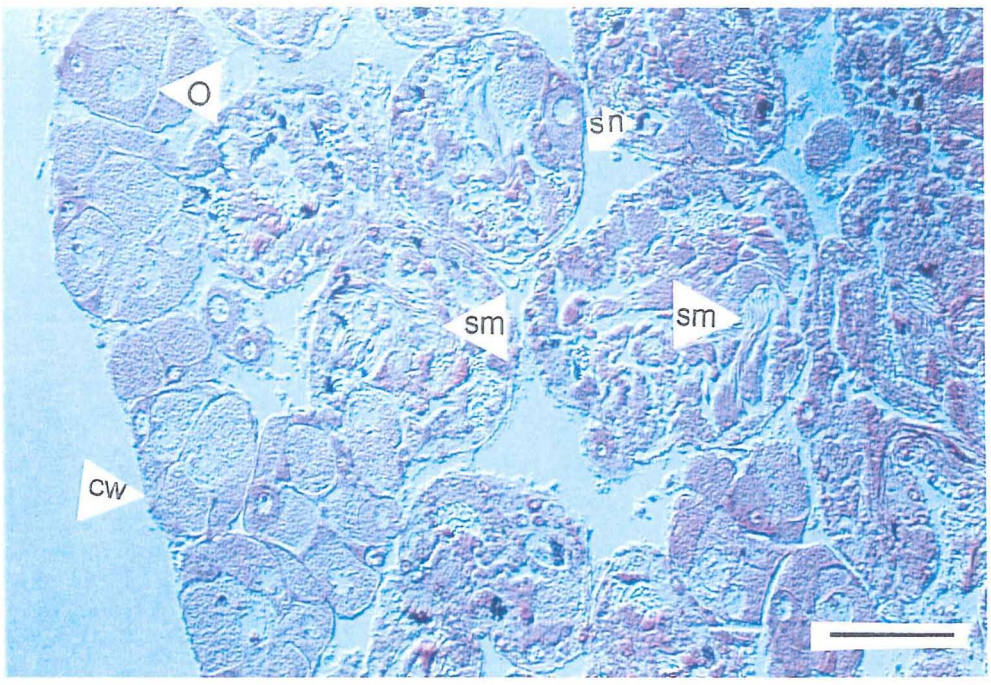


Plate 2.2: *S.zelandica* gonad showing cell wall (CW), oocytes (O), sperm material (SM), and heads of sperm (SH). Scale bar shown is 0.1mm.

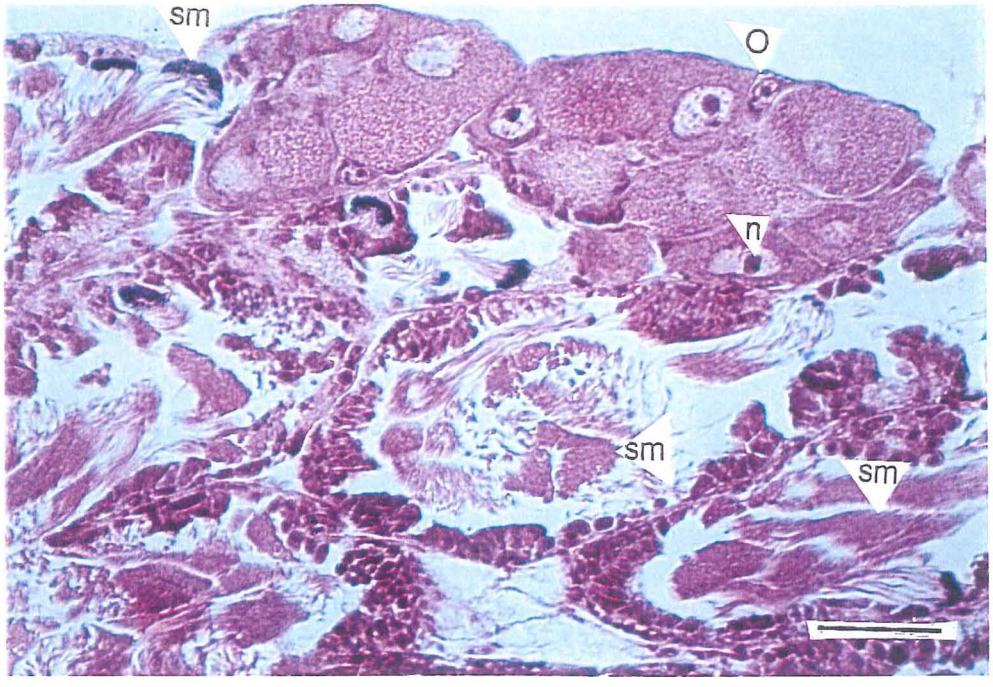


Plate 2.3: *S.zelandica* gonad showing compartments of sperm material (SM) and oocytes (O) with the nucleus visible (n). Scale bar shown is 0.05mm.

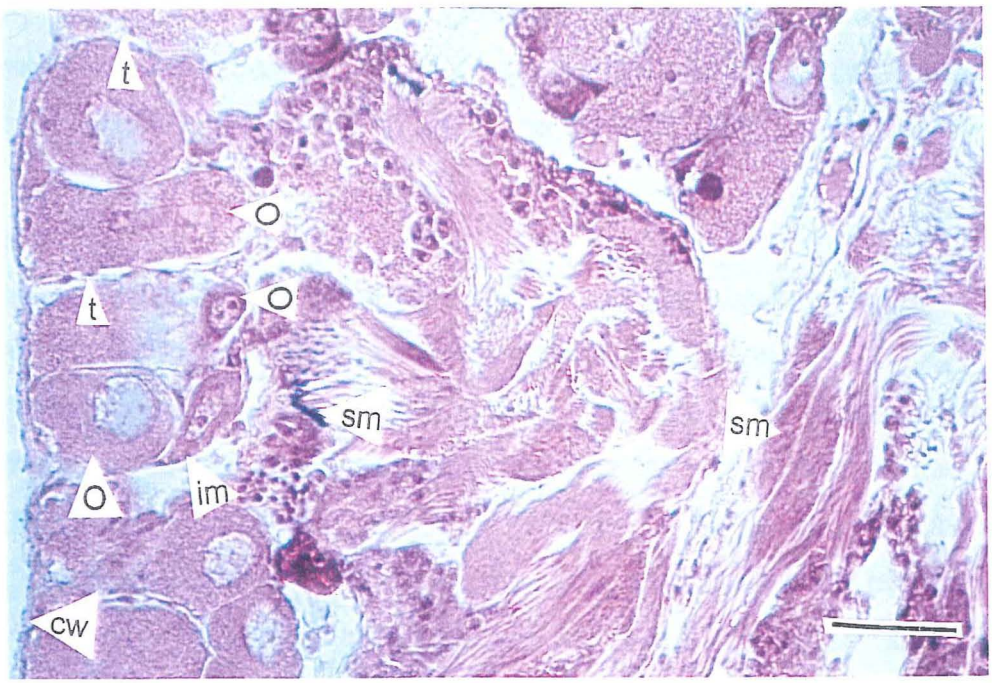


Plate 2.4: Section of *S.zelandica* gonad showing cell wall (CW), oocytes (O), sperm material (SM) traburculae (T) and immature oocytes (IM). Scale bar shown is 0.05mm.

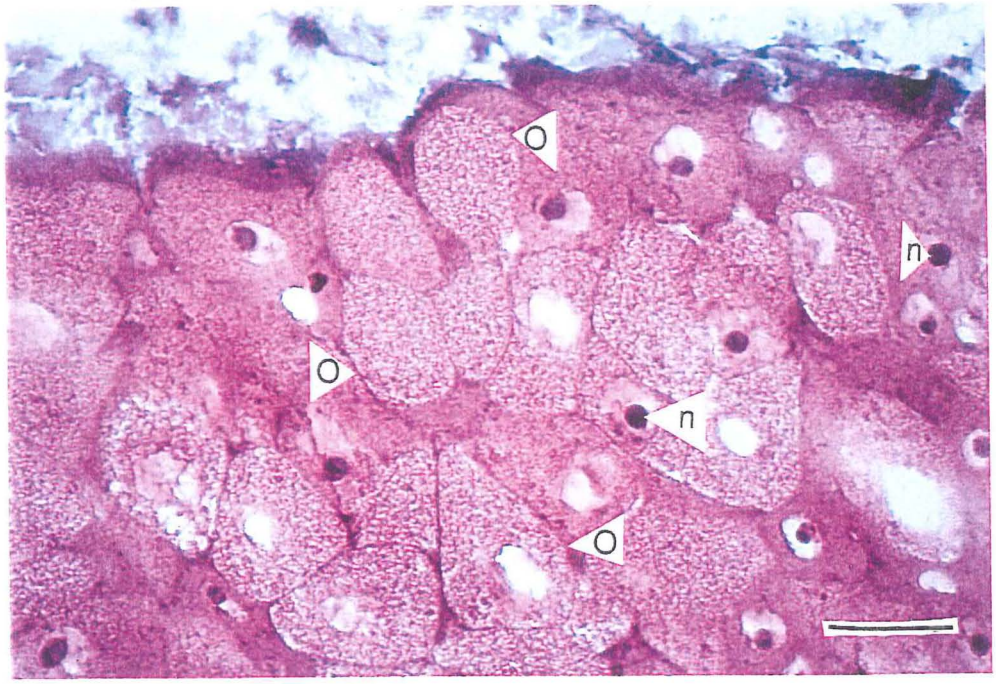


Plate 2.5: Section of *S.zelandica* gonad showing oocytes (O) with the nucleus visible (n). Scale bar is 0.05mm.

Hatching and Settlement

Egg masses took between 6 - 10 days to hatch after being laid, with the average time to hatching being 6.2 days (+/-1). After hatching the veligers died and no settlement occurred on any of the different substrate plates.

Fecundity

The mean number of egg masses laid per day per quadrat (Figure2.15) varied over a thirty days. More egg masses were laid at the end of January and early February, up to 14, than at the end of February. The mean length of egg ribbons varied with size of limpets which also gave a variation in mean number of eggs per egg ribbon (Table 2.3). The length of the egg ribbon increased with increased body size. Mean number of eggs per millimetre of ribbon did not vary much, even with different sized adults. The mean gonad weight lost from *S.zelandica* gonads (Table 2.4) also varied with the body size of the limpets. Larger limpets had larger gonads and lost more of their gonad in a spawning event.

Table 2.3: Fecundity of *S.zelandica* from egg mass collections (+/-S.E).

Mean limpet size	Mean length of egg ribbon	Mean # eggs/mm	Estimated mean # eggs/ribbon
11.6 (4.5)	4.1 (1.5)	84.6 (9.8)	304
10.82 (5.3)	3.2 (0.9)	76.3 (4.2)	244
15.4 (2.3)	6.3 (0.6)	83.6 (6.4)	514
14.24 (4.2)	5.6 (0.54)	81.6 (2.1)	468
13.34 (3.6)	4.8 (0.42)	71 (2.3)	340

Table 2.4: Mean gonad weight before and after spawning of *S.zelandica* at different size ranges.

Length	Pre-spawn weight (gms)	n	Post-spawn weight (gms)	n	Gonad weight lost (gms)
5 - 10mm	0.008	14	0.006	11	0.002
11 - 15mm	0.029	19	0.018	16	0.011
16 - 20mm	0.064	24	0.038	28	0.026
21 - 25mm	0.092	16	0.051	12	0.041

2.4 Discussion

Spatial and temporal sampling showed that at all three Kaikoura sites, *S.zelandica* occur in areas with high winter abundance of algae. This is slightly different to *S.zelandica* in northern New Zealand which have been found only on *Ralfsia verrucosa* (Jeffs, 1985). This encrusting alga is present at Kaikoura but *S.zelandica* show no preference for it. This would indicate that *S.zelandica* can occupy a wide range of habitats. It would also suggest that *S.zelandica* are indiscriminate feeders on various algal species. Intertidal gastropods can have quite different gut contents at different sites or in different seasons (Creese, 1988). Jeffs (1985) surveyed *S.zelandica* in northern New Zealand and found them predominantly on raised midshore platforms which is similar to their habitat at Kaikoura. *S.zelandica* at two sites on the Kaikoura Peninsula were found with *Cellana* spp. These large prosobranchs are also algal grazers and are possible competitors with *S.zelandica* for food and space resources. Studies in Australia have shown that Siphonaria there can cohabit with *Cellana* spp. with no deleterious effects (Underwood and Jernakoff, 1981). This is due to the different feeding mechanisms of *Cellana* spp. and *Siphonaria* spp. *Cellana* graze the substrate, removing the basal parts of the plant while *Siphonaria* leave these intact.

Size frequency and mark/recapture data suggest *S.zelandica* go through their life history fairly quickly. Growth is variable with seasons which may be due to differences in algal abundance. Growth is quicker in winter and spring which is when algal abundance is highest. Limpets at Wairepo Flats put more weight on at smaller sizes than those at Sharks Tooth Point which may be due to there being less limpets at this sites so there would be less competition for food. Growth rates from tagged limpets match the size frequency data well with small limpets growing quickly and there being a conglomeration of the mid size classes. I was unable to tag limpets smaller than 4mm so it is hard to accurately talk about juvenile growth rates. Creese (1988) suggested that it is not meaningful to consider population growth models for *S.zelandica* as size

classes are virtually impossible to distinguish. Jeffs (1985) found *S.zelandica* grew very quickly (15mmm/month) but at Kaikoura their growth was slower. Whether this is just a site difference or not is unclear.

The storm event that is shown in the mortality data indicate that *S.zelandica* cannot survive well in conditions of high loose sediment. It is unusual that the small size classes of *S.zelandica* survived better than the large but this is probably due to the fact that limpets smaller than 4mm could not be tagged and numbers of limpets at this size were hard to see. Juveniles would be the 0-5mm size class and it is likely that there is high mortality in this size range or before the veligers settle. What is not shown in this study, due to the fact that these small limpets could not be measured, is recruitment mortality (Menge, 1991). Tag loss was not a major factor as limpets were mapped and it could be seen if they returned to their home scar or not. Migration could have been a reason for loss of limpets from the population. However, as *S.zelandica* occurred in one tidal area only, migration is unlikely. In Australia shortage of food was a major factor in mortality rates (Quinn, 1988a). Even in the summer months there was some algae present at sites (see Chapter Three) so it is unlikely that lack of food is a factor in mortality of *S.zelandica* at Kaikoura. Physical factors, such as heat stress or desiccation, can also cause mortality. *Siphonaria* in South America have been found to have the ability to cool themselves and control tissue temperature to reduce physical stress (Garrity , 1984). As such stresses change with season, limpets must be able to tolerate a wide range of physical conditions (Woolcott, 1973). Wairepo Flats has longer platforms that are exposed to the air longer and receive less wave splash than Sharks Tooth. Therefore, Wairepo may be a more harsh environment and this could be a reason why there are less limpets at this site.

Most Siphonariids are hermaphrodites and *S.zelandica* is no exception. Spawning occurs throughout the year. This is seen by the abundant presence of mature oocytes in the gonad throughout the year. Egg masses could be found on the substrate at all times of the year but there were two major peaks,

which corresponded with peaks in the gonad index. Fecundity is size specific in *S.zelandica*, increasing with increased body size. Using mean number of eggs per egg mass is a coarse method of measuring fecundity (Creese, 1980a) although numbers of eggs in different sections of ribbons in this study did not vary greatly. The increase of fecundity with size is not uncommon in *Siphonaria* and has been well documented for Australian species (Creese 1980a, Quinn 1988a). Fecundity of *S.zelandica* was lower than that reported for the Australian species *S.denticulata* and *S.virgulata* (Creese, 1980a). Although size of the limpets between the two countries was similar, the length of egg masses for the Australian species was up to seven times that for *S.zelandica*. *Siphonaria* have a planktotrophic veliger larvae which is a possible reason for producing large numbers of eggs. It is documented that to survive in the plankton it is optimal to produce increased numbers of offspring (Mileikovsky, 1971). Increased reproductive output at larger sizes may explain why growth slows in the larger size ranges as more energy is put into reproductive output.

There is still an area of the life history of *S.zelandica* that nothing is known about. This is recruitment levels and survival of veligers. Although this study establishes that *S.zelandica* has an extended breeding season, size-specific fecundity and low mortality rates once settled, it is still difficult to totally determine life history without knowing about recruitment and settlement.

SECTION TWO

ECOLOGY

CHAPTER THREE

Grazing

GRAZING

3.1 Introduction

Grazers play a potentially important role on the intertidal shore by being a major regulatory force on algal growth and abundance. Limpets are a particularly well studied group of grazers (see reviews by Branch 1981 &1986, Hawkins and Hartnoll 1983), although pulmonates less so than prosobranchs. The upper limits of algal distribution on a shore may be governed predominantly by physical factors, while biotic interactions are more important in setting low shore limits (Dayton 1971, Lubchenco 1980, Branch 1986). However, these are mitigated by many other variables including larval distribution (Menge, 1991) and space available for settlement or settlement processes (Dayton 1971, Menge 1976). Some studies have shown that the physical factors become important only when the biotic factors, such as grazing, are reduced (Jernakoff, 1983). There are many cases where grazers rather than physical factors can control the upper limits of algae in Australia (Underwood 1980, Jernakoff 1983). In an ungrazed situation, where limpets have been removed, one general pattern of algal colonisation, in eastern Australia, is that diatoms appear first, rapidly followed by ephemerals, then perennial fucoids (Sousa 1979, Underwood 1980). There are some documented differences between algal colonisation rates in different seasons, usually with colonisation occurring more rapidly in winter than in summer (Emmerson and Zedler 1978, Cubit 1984, Quinn and Ryan 1989, Beovich and Quinn 1992, Dye 1995).

It is widely accepted that grazers have a large impact on type and amount of algae on the shore, not only in a negative way but also positively. There are numerous studies on how introduction of limpets can affect the algal colonisation process (Lubchenco 1978, Duggins and Deithier 1985, Farrell 1988, Beovich and Quinn 1992, Bendetti-Cecchi and Cinelli 1993, Scheibling 1994). In brief, the effects seem to be in the order or pattern of re-establishment of algae (Beovich and Quinn, 1992), in the abundance and

intensity of competition between plants (Duggins and Dethier, 1985) or in inhibiting colonisation in the first place (Geller 1991, Liu 1993). The composition of an algal stand and its species richness is also affected by grazing (Farrell 1988, Bendetti-Cecchi and Cinelli 1993, Liu 1993, Scheibling 1994). A general summary of herbivores effects on algae are that they affect a) abundance, b) species richness and diversity, c) zonation and d)intensity of competition (Duggins and Deithier, 1985) although Dayton (1975) concluded that molluscan herbivores had little, if any effect on algal succession in some northwest Pacific sites. Farrell (1988) concluded that the community that developed when limpets were removed was not a persistent alternate state, while Southward (1964) found that there was a cyclic relationship on the shore between grazers and algae and that the appearance of the shore at any one time is due to stability in this cycle. Differences in algal colonisation rates, species richness and diversity may vary widely between and within countries and hemispheres.

Grazer studies seem to be in agreement that limpets prefer ephemeral species of algae, such as *Ulva* species (Jernakoff 1985, Bendetti-Cecchi and Cinelli 1993, Liu 1993), and that in the absence of limpets these species become well established, even outcompeting perennial species of algae (Lubchenco, 1978). It is not only macroalgal abundance that is important but also the microalgal film found on the substrate. The propagules of macroalgae settle and germinate within this layer (Hill and Hawkins, 1990) so the grazing effect can start here. It has been demonstrated that removal of limpets causes an increase in microalgae, in the same way that a removal of grazers can cause macroalgal abundance to increase (Nicotri, 1977). The most effective way to measure microalgae is by taking chlorophyll samples from the substrate (Underwood and Jernakoff 1981, Underwood 1984, Hill and Hawkins 1990). Some algae have defence systems against grazers which enable them to thrive even in the presence of grazers. These defences include morphological, such as growing to large to be eaten or forming a crustose growth, or life history adaptations, such as a change in time of spawning (Duggins and Dethier,

1985). The above examples are possible negative effects of limpets on algae although Underwood and Jernakoff (1981) found that even very high densities of *Siphonaria* had no effect on the colonisation and growth of algae in Australia. The positive effect that limpets may have on algae are that crustose algae may depend on grazers to stop being overgrown by foliose algae (Dethier 1994). Grazers can create an open space for spores to settle or may disperse some opportunistic algal species via their survival in the gut/faecal products of the limpets (Santelices and Correa 1985). *Siphonaria* species are croppers rather than scrapers in their feeding mechanism and usually consume macroalgae while leaving the basal parts of the plant intact (Underwood and Jernakoff 1981, Creese and Underwood 1982, Beovich and Quinn 1992, Laisaik and White 1993). In the studies that have been done outside of New Zealand (Table 3.1) on *Siphonaria* grazing, there are varying results. Some found that while *Siphonaria* could keep algal abundance down, they did not significantly reduce algal cover in experimental plots (Underwood and Jernakoff 1981, Creese and Underwood 1982), yet others found that *Siphonaria* species could reduce algal cover of certain species (Beovich and Quinn 1992, Laisaik and White 1993). In his study on *S.zelandica*, Jeffs (1985) found that the limpets only occurred on patches of the encrusting algae *Ralfsia verucosa* and that this alga was the main gut constituent of the limpets, a result that is contrary to all other studies on *Siphonaria* species.

Table 3.1 Grazing studies carried out on *Siphonaria* species worldwide.

Authors	Year	Country	Species
Underwood and Jernakoff	1981	Australia	*S.denticulata*
Cook & Cook	1981	Bermuda	*S.normalis & S.alternata*
Creese & Underwood	1982	Australia	*S.virgulata & S.denticulata*
Jeffs	1985	New Zealand	*S.zealandica*
Beovich & Quinn	1992	Australia	*S.diemensis*
Lasiak & White	1993	South Africa	*S.concinna*

There is much debate over whether the density of animals in populations is determined by food availability, larval abundance, settlement patterns or by physical constraints. In general when the density of a grazer is increased,

physical constraints. In general when the density of a grazer is increased, there is a corresponding decrease in survival and growth rates of the animals (Petratis, 1992). Several studies that have manipulated *Siphonaria* species density have found conflicting results. Creese and Underwood (1982) found that increasing the density of limpets led to reduced growth and a decrease in the tissue weight of limpets but the authors also found no significant increase in mortality. This led them to conclude that intraspecific competition is probably not an important factor in regulating *Siphonaria's* abundance. On the other hand a study by Lasiak and White (1993) found high mortality at increased densities of *Siphonaria* although this may have been due to physical stresses. Yet in their discussion, Laisaik and White claim *Siphonaria* species can tolerate increased density of their own species for prolonged periods of time. This agrees with a study on *Siphonaria gigas* (Ortega, 1985) where increased density led to reduced body weight but the limpets tolerated conditions of high density for considerable time periods.

New Zealand shores are considered to be different to the extensively studied northern hemisphere shores. Here there is no large fucoid canopy although *Hormosira banksii* is dominant in most New Zealand mid intertidal areas (Raffaelli, 1979). *Ralfsia* is also abundant and there are patchily distributed areas of ephemeral species (Creese, 1988). In his 1988 review, Creese concluded that most intertidal limpets in New Zealand are generalist grazers, although what they eat may vary with season and site. From this he proposed that it is difficult to show if food is a limiting resource as it is difficult to ascertain a precise diet in an indiscriminate feeder.

At Kaikoura *Ralfsia* is patchy in its abundance and distribution and the mudstone platforms are dominated by the typical eastern coast of the south island platform structure (see Chapter Two) but *S.zelandica* occur in large numbers in the mid-tidal zone all year round. My aim was to investigate *S.zealandica's* grazing effect on the shore at Kaikoura and to determine how different densities of limpets affect both algae and limpet mortality.

3.2 Materials and Methods

Density Experiments

Doubling the ambient density of the limpets should result in less algal cover than in treatments with ambient, half-ambient or no limpets. Changing the density of the limpets could result in mortality and weight differences in limpets among treatments. By measuring the weight of limpets at the beginning and end of the experiment overall weight differences can be detected. This experiment was tested the effects of densities at two sites - Wairepo Flats on the northern side of the peninsula and Sharks Tooth Point on the south side. There may also be site-specific differences in responses to densities. Both sites consist of long sloping platforms and were relatively bare of algal cover at the start of the experiment. The densities were: ambient (30 limpets/0.25m^2), 1/2 ambient (15/0.25m^2), double ambient (60/0.25m^2) and no limpets. These tested to see if there is a density dependant effect on the limpets mortality, weight and the effect of increased concentrations of grazers on the algae. Exclusion treatments show how well the algae survives without grazing pressure and half ambient densities show if algae can flourish with reduced grazing pressure.

Vexar™ plastic mesh fences, with a hole diameter of seven millimetres, enclosed an area of 0.25m^2 of substratum. The sides were five centimetres high and there was a three centimetre turnout flap at the bottom to enable the fences to be attached to the substratum. Plate 3.1 and 3.2 show fences *in situ* at the Sharks Tooth site in winter and spring/summer.

Fences were attached to the substratum by first putting a strip of Selleys Brick and Concrete Silicone™ onto the substrate before placing the fence onto this. A strip of plastic tape was put along the side of each fence and secured along its length with Ramset™ 30mm concrete nails. The corners of the fence were secured to the ground by drilling a 40mm hole in the substrate using a compressed air drill (Plate 3.3) into which 40mm Ramsett™ plastic tappets were hammered.

Plate 3.1: Density experiment *in situ* at Sharks Tooth in winter showing abundance of green algae (a mix of *Ulva/Enteromorpha* species).

Plate 3.2: Density experiment at Sharks Tooth showing reduced algal cover.

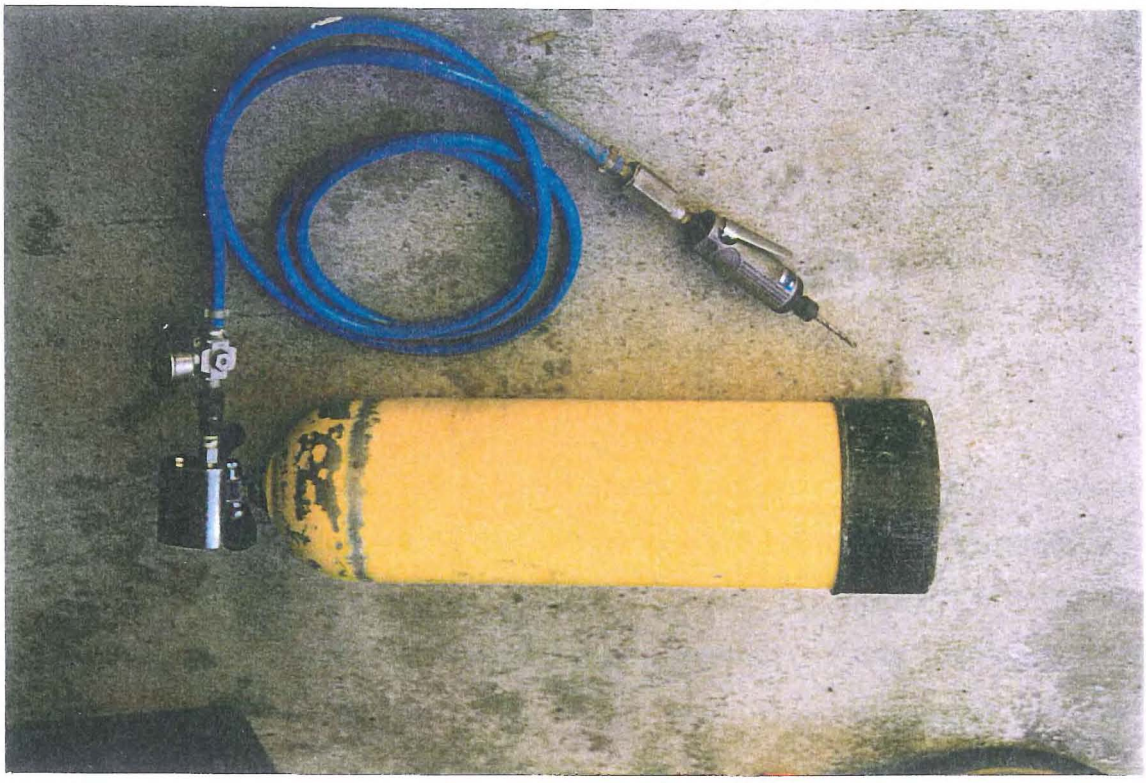


Plate 3.3: Compressed air drill attached to S.C.U.B.A tank used to drill holes in substratum for grazer density experiment.

Table 3.2 Density Experiment set-up showing type of fences for treatments, the number of limpets per treatment; n=5.

Treatment	Fence Type	Number of Limpets
Ambient density	Four sided	30
Half ambient density	Four sided	15
Double ambient density	Four sided	60
Exclusion	Four sided	0
Half Fence control	Two sides	24 - 36
Open control	No sides	24 - 36

Various densities and treatments were used (Table 3.2) to test grazing pressure effects and intraspecific density effects. Once the fences were on the shore the densities were randomly assigned except in the half controls (Plate 3.4) and the open controls (Plate 3.5). Limpets used were initially all in the same size range of 14 - 18mm in length.

The fences were left for a month with treatments in place before measurements were started. During the course of the experiment fences were checked weekly to clear any build-up of algae around the outside and to replace any nails that had become dislodged. The experiment was monitored monthly, for eleven months, for percent cover of algae of each species. The number of limpets in each treatment was counted and density levels maintained for the duration of the experiment.

Chlorophyll Sampling

Chlorophyll sampling was done to determine amounts of microalgae present because algal films on the soft rock could be measured in no other way (Underwood 1984, Hill and Hawkins 1990). Every three months from all the treatments and controls in the density experiment, three $1cm^2$ areas of substrate were removed using a flat ended chisel (the head of the chisel was exactly one centimetre long). Sections from the same replicate were kept together in glass vials before ten millilitres of 90% acetone was poured into each vial and the sections were crushed with a mortar and pestle, after which the mixture was put into a clean glass vial and left in a dark fridge for twenty four hours to extract the chlorophyll.

After 24 hours the sample was filtered through glass fibre paper into a clean glass vial. The resulting fluid was analysed in a spectrophotometer (Underwood 1984, Hill and Hawkins 1990), the Kontron Uvikon 860, with wavelengths set to 665 and 750. The formula used to determine how much chlorophyll there was in each sample was:

$$\text{chla } (ug/cm^2) = \frac{11.9 \times \text{absorption reading} \times 10ml}{3cm^2}$$

(HMSO, 1986)

Growth and Mortality

Density affects growth and mortality of organisms, presumably because of food limitation. To investigate the effects of different densities, five limpets in each fence were tagged at the beginning of the experiment and length was measured monthly. At the end of the experiment five limpets from each

treatment (the tagged ones, where possible) were removed, taken to the lab and dissected from their shells. They were then dried at 30°C to a constant weight and weighed. Mortality was also measured each month by counting the number of remaining limpets. Any limpets that were used to replenish numbers were paint-marked for identification.

3.3 Results

Percentage Algal Cover

When the density experiments were started in April, all treatments were scraped clear of algal cover, so initial percentage cover is zero. Percentage cover of algae in all treatments increased over the next three months to at least 70% cover at Sharks Tooth but not all increased at Wairepo (Figure 3.1). Levels of algae remained high for the months of July to October before decreasing over summer. Percentage cover of algae differed between the two sites and between treatments. This was confirmed by Wairepo having less algal cover in all treatments especially over summer (November - February). Analysis of variance done at the end of the experiment showed a highly significant difference between sites ($p<0.000$) and treatments ($p<0.000$) (Table 3.3). At Sharks Tooth the 60 limpet treatment only had a maximum of 70% cover in winter that dropped back to 40% and less over spring and summer. However at Wairepo there was more algae in this treatment than over the course of the experiment than there was in the 60 limpet treatment at Sharks Tooth. All treatments at Sharks Tooth had a quick initial increase in percent cover over the first four months with them all reaching maximum cover in July. All treatments at this site other than 60 limpets never had less than 40% cover after the first two months. The fence control had the highest amount of algal cover over time with the zero limpet treatment being very similar. Both these treatments and the open control had 100% algal cover over the winter months of June - October.

At the Wairepo site no treatment ever had 100% cover and the initial two months did not show a rapid increase in algae. The 60 limpet treatment had

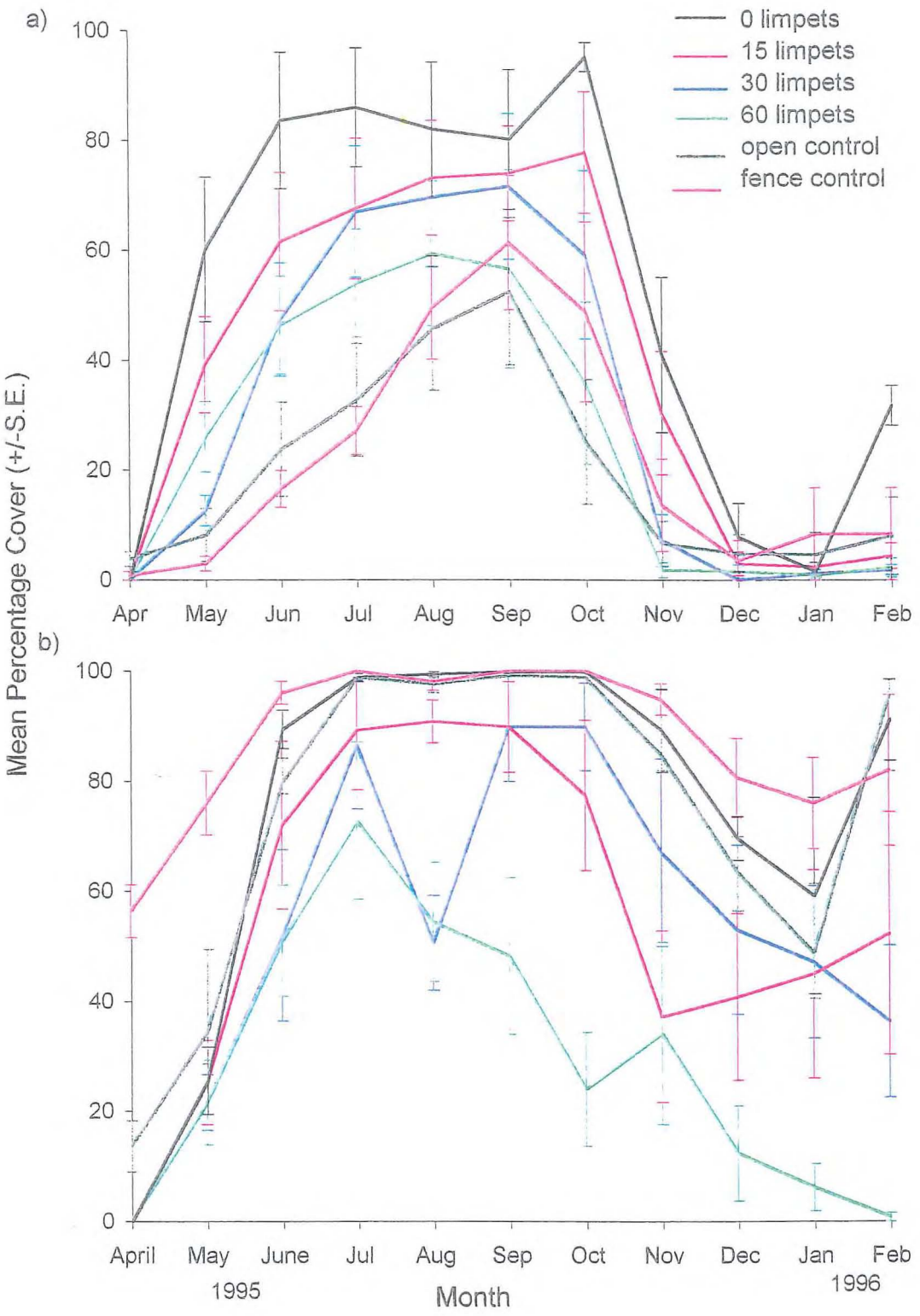


Figure 3.1: Mean Percentage Cover of Total Algae in density experiment treatments at a) Wairepo Flats and b) Sharks Tooth from April 1995 to February 1996.

when it had very little (<5%). The other treatments fell into an order of increasing algal cover from 30 to 15 to 0 limpets. Zero limpets had more than 80% cover for most of winter (June - October) but like all treatments at this site there was a sharp decrease in percent cover in October/November to very low levels (<20%). Figure 3.2 shows the analysis of variance data plotted showing clearly the site differences in all treatments except 60 limpets, and the treatment differences. The ANOVA results showed that percent cover in a treatment is dependent on site by having a significant site x treatment

Table 3.3: Analysis of Variance for percent total algal cover data for Sharks Tooth and Wairepo Flats, February 1996. Variances homogeneous (Cochrans test, p>0.05). Main effects in bold, interaction abbreviations: S = site, DT = densities treatments, C = controls.

Source	df	SS	MS	df error	MS error	F	p
Btwn all Densities (+ controls)	5	22162.0	4432.4	48	443.36	9.997	0.000
Control vs. all others	1	4762.8	4762.8	48	443.36	10.74	0.001
Between C	1	231.2	231.2	48	443.36	92.16	0.000
Btwn DT	3	17168.0	5722.6	48	443.36	62.40	0.000
Btwn sites	1	32387.2	3238.2	48	443.36	73.048	0.000
S xDT	3	4337.1	1445.7	48	443.36.	3.460	0.027
S x C	1	1126.8	1126.8	48	443.36	0.414	0.529
S x C vs.DT	1	4762.8	4762.8	48	443.36	10.742	0.019
Site x Treatment	5	10226.7	2045.5	48	443.36	4.613	0.001
Residual	48	21281.6	443.3				
Total	59	86057.5					

interaction (Table 3.3). Pre-planned comparisons showed that there was a significant difference in the site x density treatment interaction (excluding controls). The significant difference between treatments was also broken into components where the difference was found to be between the noncontrol and between the control densities. The ANOVA shows that there is a difference within and between treatments that varies with site.

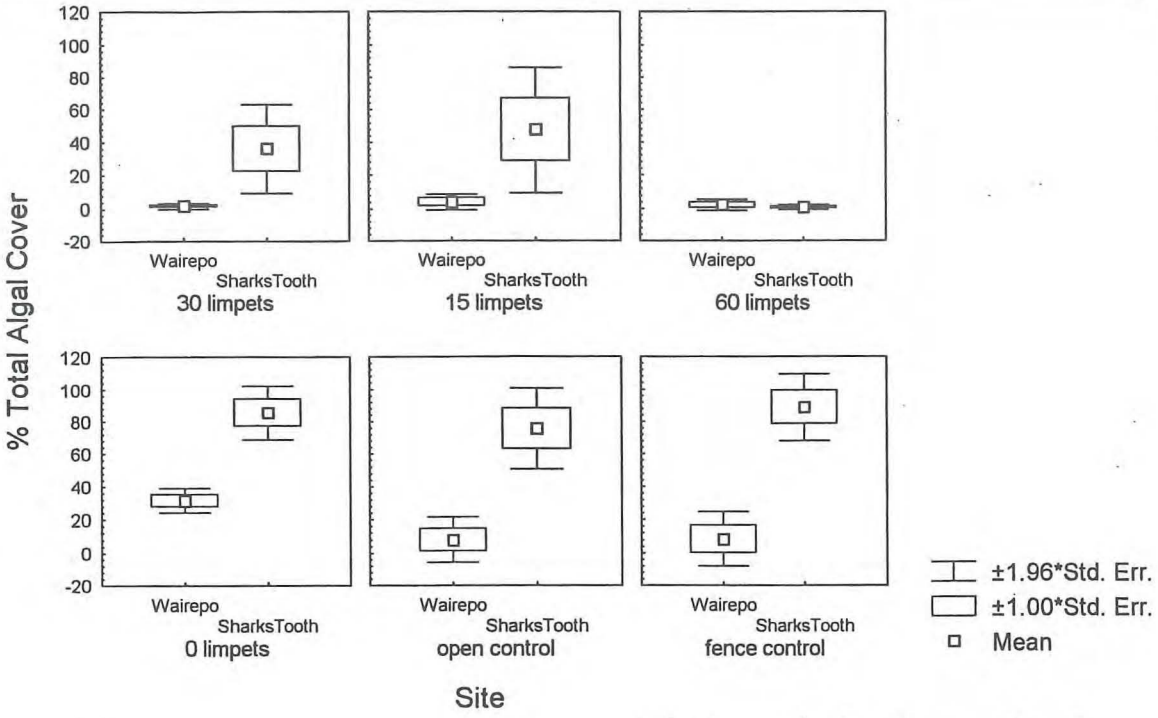


Figure 3.2: Box and whisker plots for total algal cover in density experiment treatments for February 1996.

Percent cover of specific algal species were measured within total algal cover (Figure 3.3, 3.4). *Scytosiphon lomentaria* had greatest abundance at Sharks Tooth in June-August but slightly later at Wairepo (August-September). At Sharks Tooth the two controls had up to 95% cover and were higher than all the density treatments. The treatments were all similar and there was no significant difference between them (see Appendix C for ANOVA data) although there was a significant difference between sites. Clearly there was a difference between sites in both the magnitude and time of the grazing effect on *S.lomentaria*. At Wairepo the controls had the least amount of *S.lomentaria* and 0 limpets had the most. Again the other treatments were all similar to each other and fell between the controls and zero limpets. Plates 3.6 - 3.9 show *Scytosiphon* in different density treatments at Sharks Tooth in July. *Porphyra* species is not abundant at either site for most of the year, reaching greatest abundance in July with up to 30% cover. It appears at both sites later than *Scytosiphon* and the peak abundance differs between sites but not significantly. At both sites the only treatment that had a high abundance of *Porphyra* species is zero limpets, although at Sharks Tooth both 30 limpets and fence controls had a pulse of 20%. This lasted only one month in both these treatments.

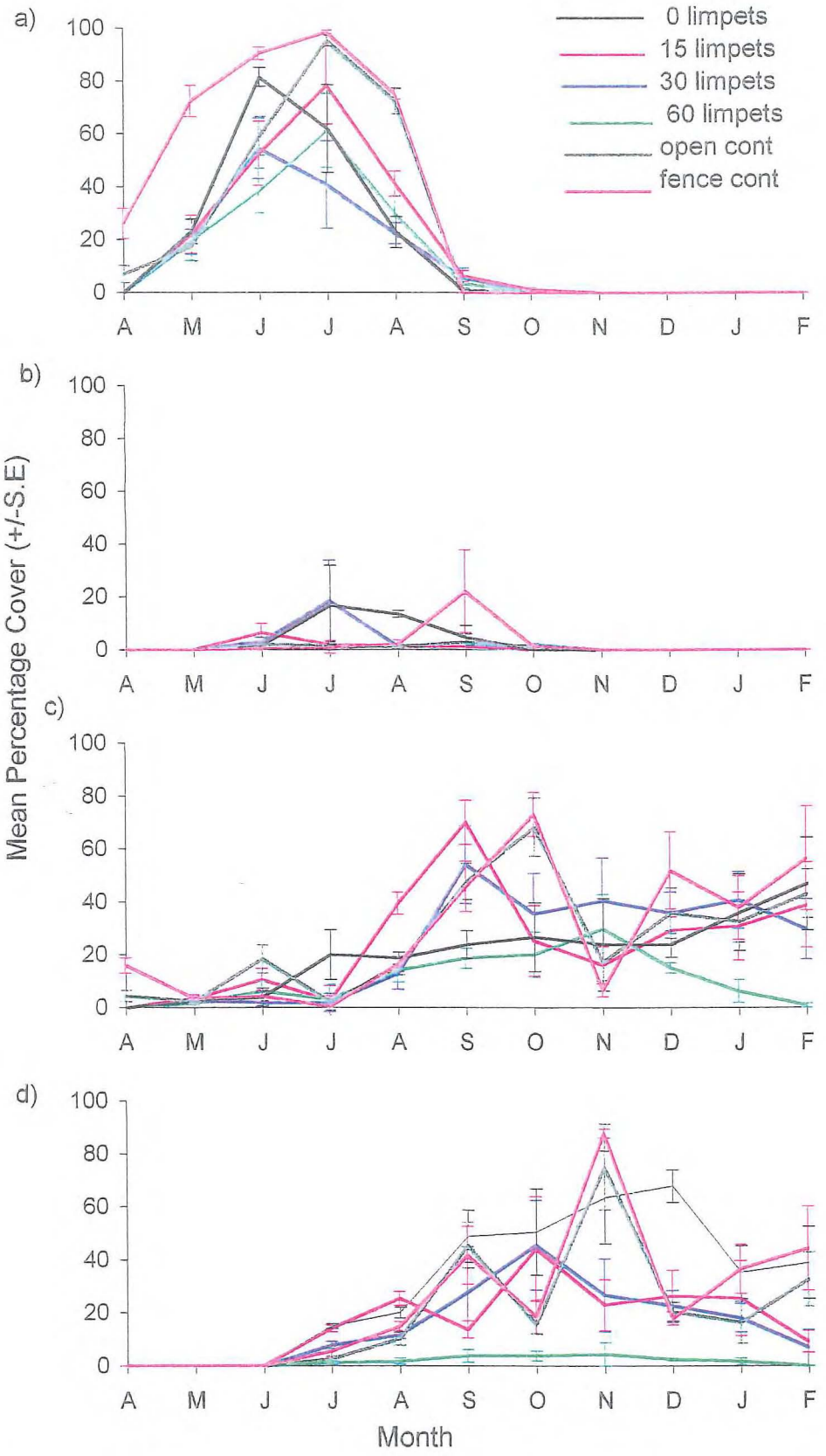


Figure 3.3: Mean percentage cover of a) *Syctosiphon*, b) *Porphyra*, c) *Ulva/Enteromorpha* and d) algal film in density experiment trearments at Sharks Tooth Point from April 1995 to February 1996.

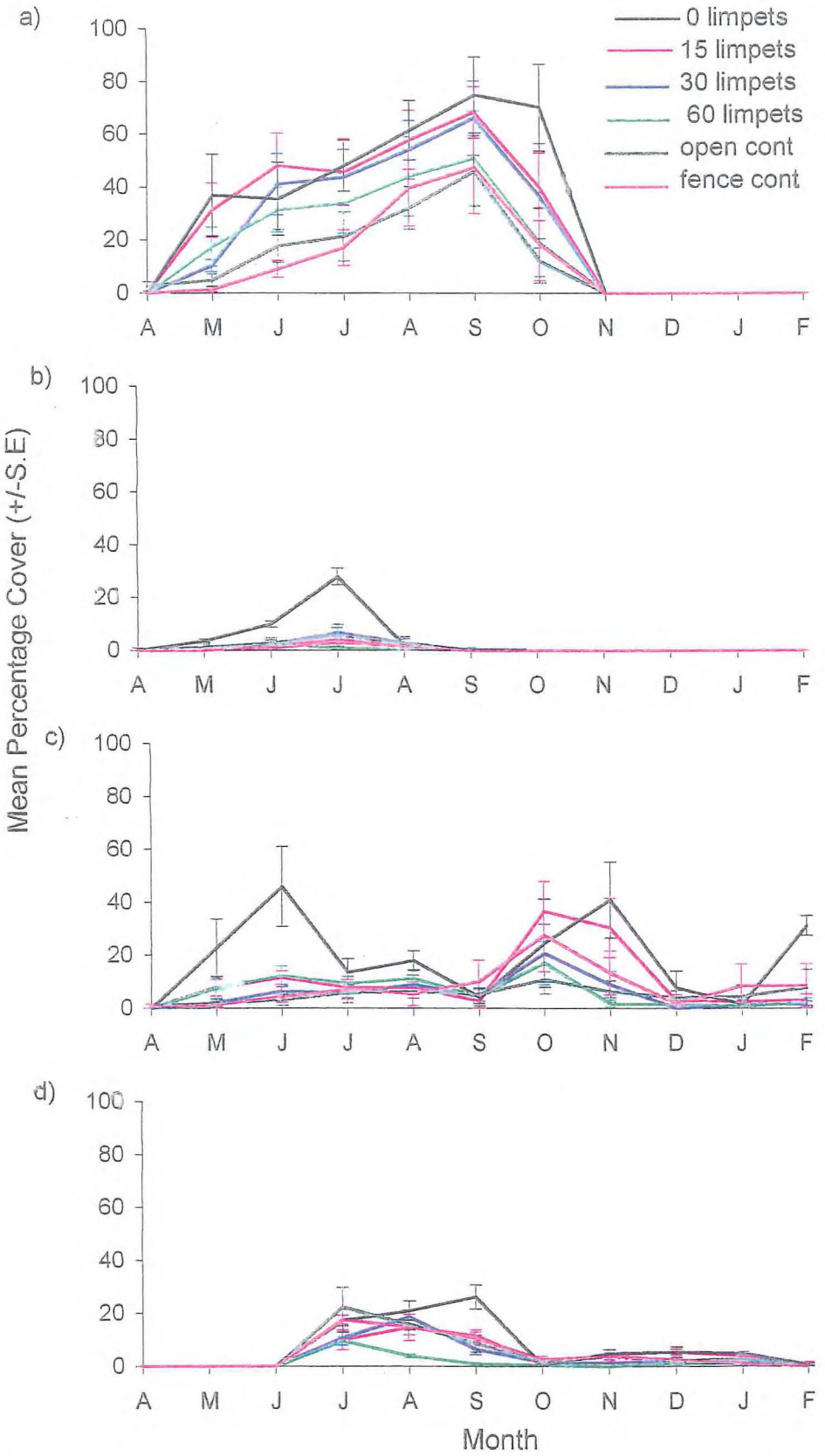


Figure 3.4: Mean percentage cover of a) *Syctosiphon*, b) *Porphyra*, c) *Ulva/Enteromorpha* and d) algal film in density experiment trearments at Wairepo Flats from April 1995 to February 1996.

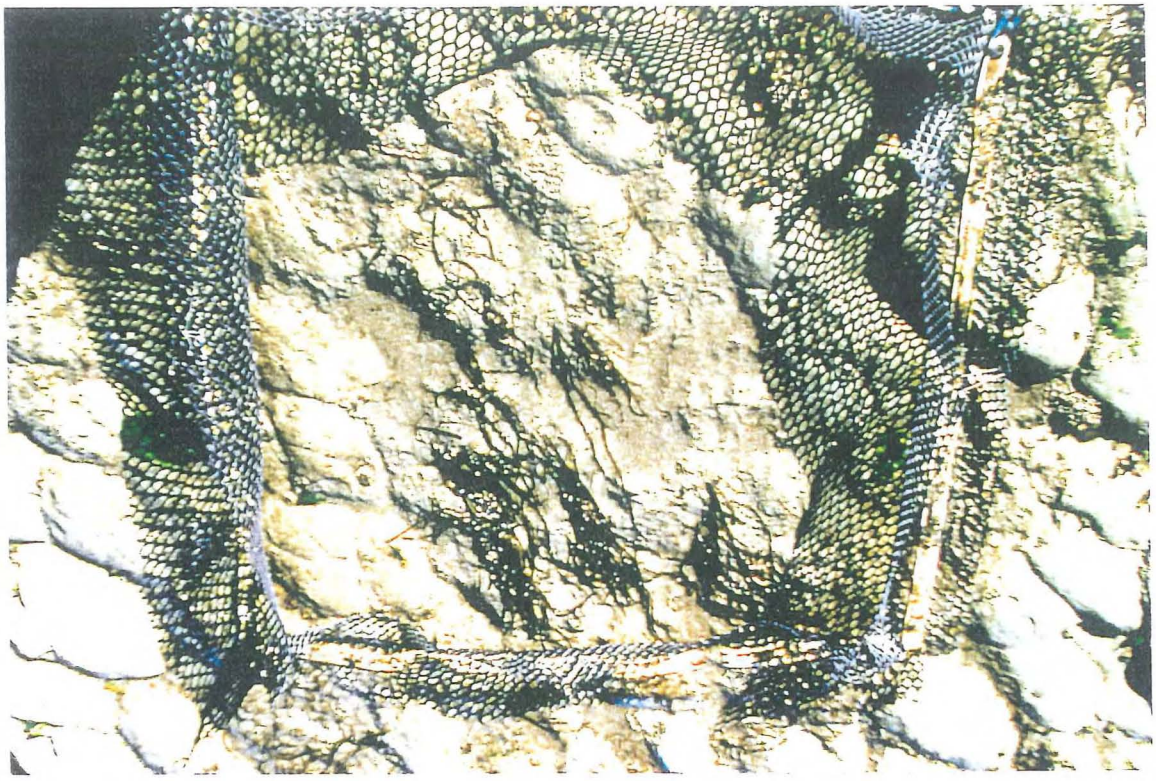


Plate 3.6: Density experiment: 30 limpet treatment at Sharks Tooth in July showing *Syctosiphon lomentaria* density.

Plate 3.7: Density experiment : 15 limpet treatment at Sharks Tooth in July showing *Scytosiphon lomentaria* abundance.

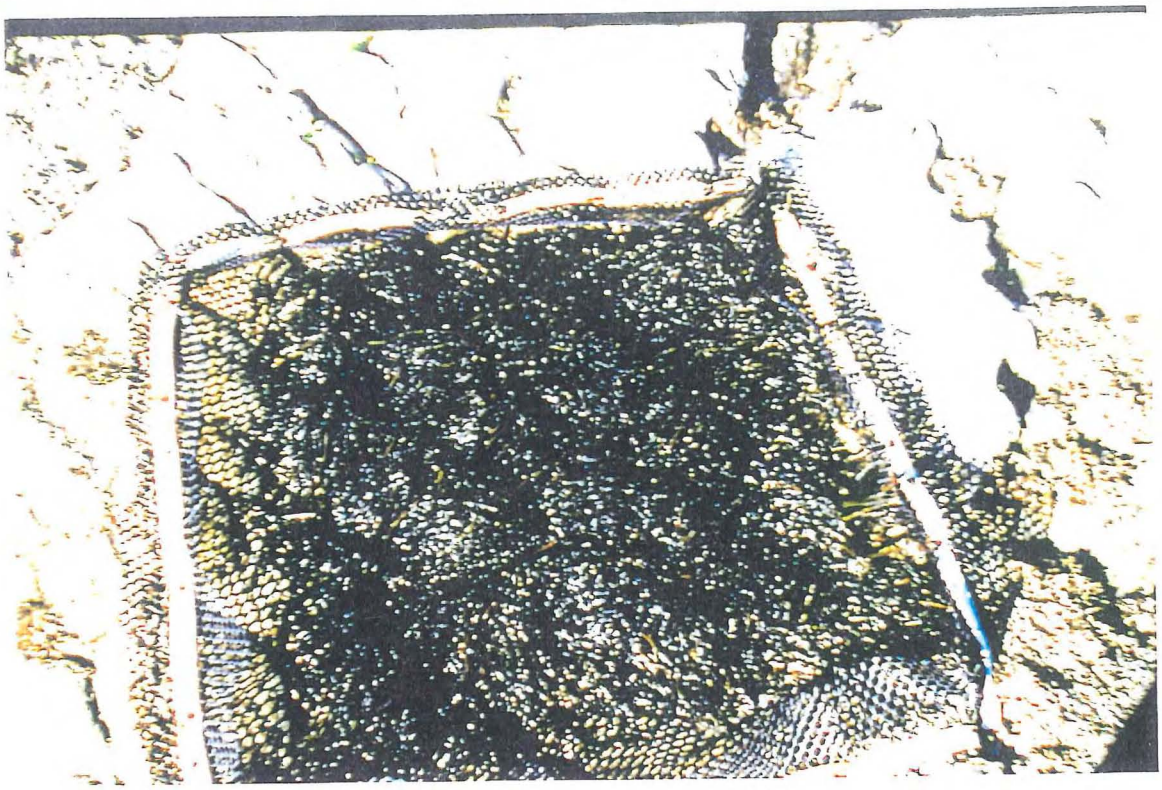


Plate 3.8: Density experiment: 0 limpet treatment at Sharks Tooth in July showing *Syctosiphon lomentaria* abundance.

Plate 3.9: Density experiment: 60 limpet treatment at Sharks Tooth in July showing *Syctosiphon lomentaria* abundance.

The *Ulva/Enteromorpha* complex started appearing at both sites after the main peak of *Scytosiphon* and *Porphyra*, and were not present until three to four months into the experiment, in the month of July. At Sharks Tooth these green algae were present to the end of the experiment in February at both sites, but with less abundance at Wairepo (<40%). At this site there was also a sharp decrease in abundance between September/October. At Sharks Tooth there is a difference in treatments with 60 limpets having very little cover (<10%) while zero limpets had the most with 50% and higher, except in November when the two controls had 90% cover. There was little difference between 15 and 30 limpets. Therefore, there is an increasing percentage cover of algae with decreasing density. Wairepo had similar results to Sharks Tooth. The zero limpet treatment and controls had the most cover at 40%, while the 15 limpet and 30 limpet treatments having similar cover to each other of 20%. The sixty limpet treatment has the least cover of green algae, no more than 10%. The last algae group looked at was algal film (red/crustose alga). Although its abundance is variable over time it is always present in all treatments at both sites. Sharks Tooth tended to have more algal film (up to 70%) than Wairepo (maximum 40%). Fifteen limpets and the two control treatments at Sharks Tooth had quite high amounts in September (65%) and October (70%) respectively with both decreasing sharply after this peak. Zero land 60 limpets both had low levels (<30%) for the duration of the experiment until December when 0 limpets increased up to 50% in February while 60 limpets decreased down to 0% at the same time. At Wairepo Flats 0 limpets generally had 10 - 20% more algal film than the other treatments. The density treatments all had fairly similar levels except in October/November when 15 limpets had an increase to 30% cover. ANOVA results showed a significant difference between treatments and sites (see Appendix C). Analysis of variance indicates that there is a statistically significant difference in density treatments.

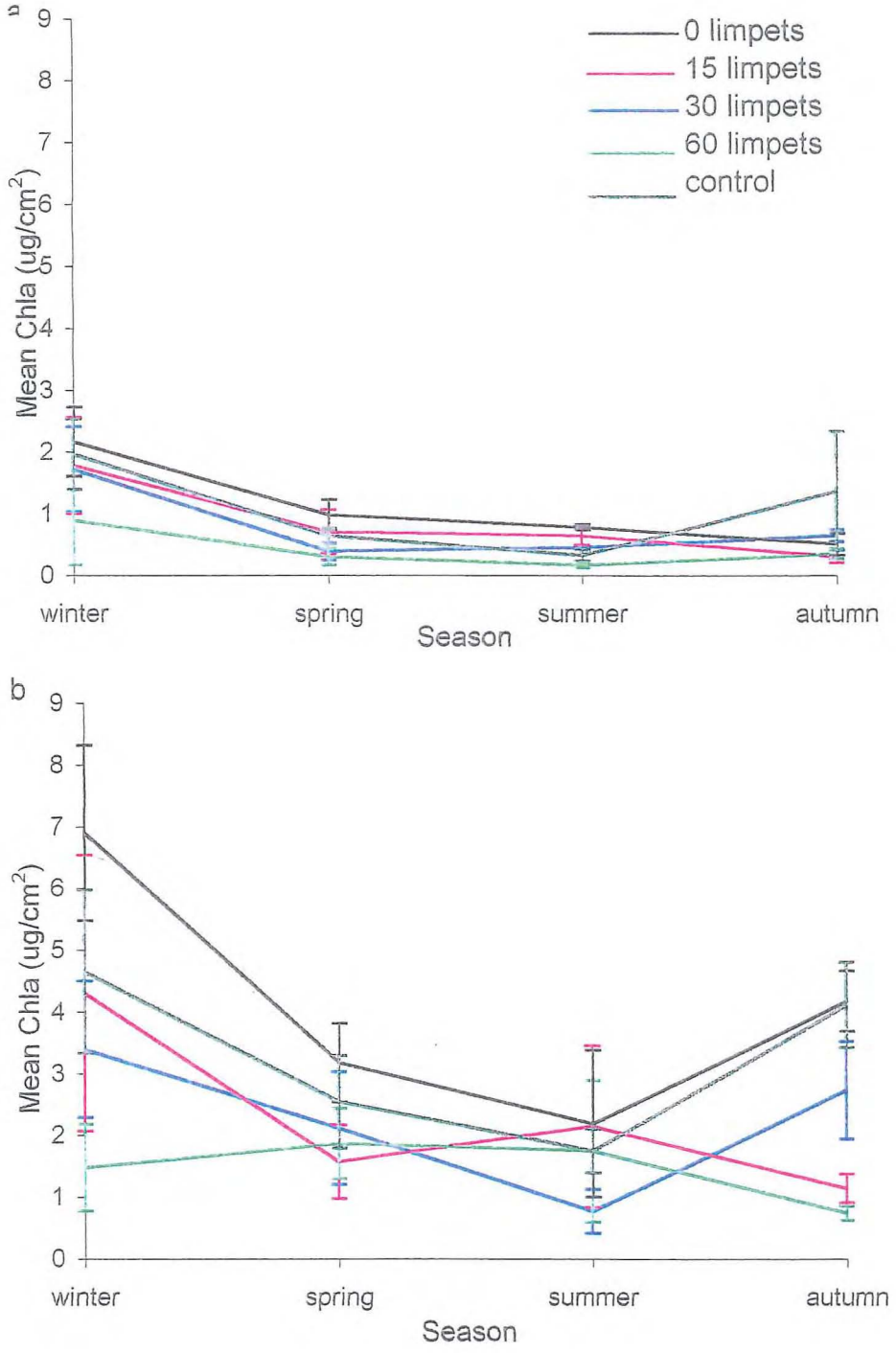


Figure 3.5: Mean chlorophyll (u g/cm^2) (+/-S.E) per season for a) Wairepo Flats and b) Sharks Tooth Point from density experiment treatments.

Chlorophyll Sampling

Chlorophyll analysis showed that although the treatments do not vary widely over seasons there was a significant difference between sites (Table 3.4). In Figure 3.6 it is shown that there is more chlorophyll on average in density treatments at Sharks Tooth (1.5*u*g - 7*u*g) than at Wairepo (0.9*u*g - 2.1*u*g). At both sites the zero limpet treatment had the highest level of chlorophyll. At Sharks Tooth the chlorophyll concentration in the zero and two control treatments drops sharply from winter to spring. A further decrease occurred in the zero limpet and open control treatments from spring to summer followed by an increase in autumn. The fifteen limpet treatment decreased until spring,

Table 3.4: Analysis of variance table for chlorophyll data in autumn. Variances are homogenous (Cochrans test, p>0.05). Main effects in bold, abbreviations: DT = density treatments, S = site, C = controls.

Source	df	SS	MS	df error	MS error	F	p
Between all treatments (+ controls)	4	39.40	9.85	40	1.21	8.12	0.000
C vs.DT	1	16.99	16.99	40	1.21	6.62	0.013
Between DT	3	22.40	7.46	40	1.21	3.92	0.016
Between sites	1	47.60	47.60	40	1.21	39.28	0.000
SxC	1	1.94	1.94	40	1.21	62.17	0.000
SxDT	3	15.36	5.12	40	1.21	9.07	0.000
SxC vs.DT	1	1.98	1.98	40	1.21	14.02	0.000
Site x all treatments	4	19.28	4.82	40	1.21	3.98	0.008
Residual	40	48.44	1.21				
Total	49	154.72					

increased in summer before decreasing again. The thirty limpet treatment decreased from winter through to summer before increasing again in autumn. In contrast, the 60 limpet treatment increased to spring and stayed stable until a decrease in autumn. At Wairepo all the treatments decreased from winter to summer before having a slight increase in autumn. The treatment significance revealed in the ANOVA is both within noncontrol densities and between the control and noncontrols (Figure 3.7). Wairepo, in comparison to Sharks Tooth,

had much less chlorophyll at all times of the year in all treatments. This site did not have the fluctuations seen in all treatments at Sharks Tooth.

Size and Mortality

The size of limpets was measured as dry weight. There was a significant difference between sites (Table 3.5) but not between treatments. This can be seen in Figure 3.7 where there is little difference between end controls and beginning controls at either site. Sharks Tooth, however, had much heavier limpets in the controls than at Wairepo. In the three density treatments this trend is also true but not to such a great extent. Of these the 15 limpet treatment had slightly higher weights than 60 or 30 limpets but this result was not significant although there is a site difference. At Wairepo there was no difference between 60 and 30 limpets which is the same at Sharks Tooth

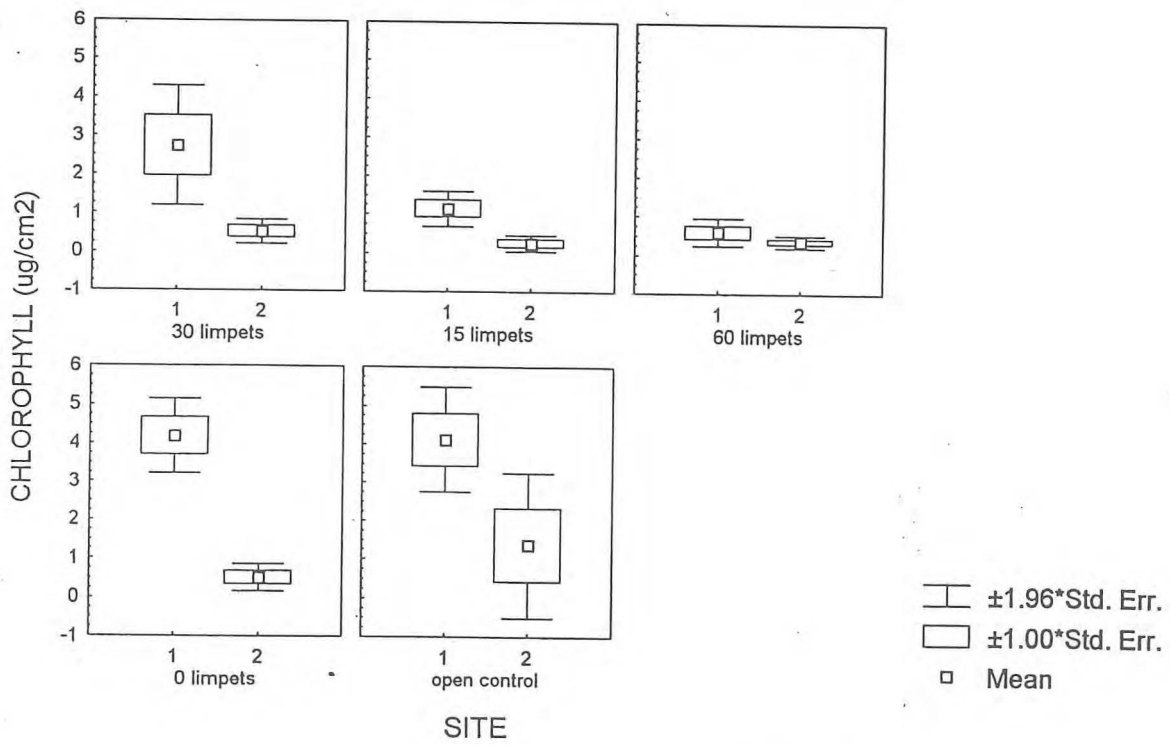


Figure 3.6: Box whisker plot for mean chlorophyll amounts in density experiment treatments for autumn (April 1996). Site 1 is Sharks Tooth and 2 is Wairepo Flats.

Table 3.5: Analysis of Variance table of dry weights of limpets in density experiment treatments from Wairepo Flats and Sharks Tooth, February 1996. Variances homogenous (Cochrans test, p>0.05). Main effects in bold, abbreviations: C = control, DT = density treatments, S = site.

Source	df	SS	MS	df error	MS error	F	p
Between all treatments (+C)	3	0.0022	0.0007	32	0.0003	2.33	0.092
C vs. DT	1	0.0005	0.0005	32	0.0003	0.79	0.379
Between DT	2	0.0016	0.0008	32	0.0003	2.28	0.121
Between Sites	1	0.0094	0.0094	32	0.0003	29.7	0.000
S x C	1	0.0009	0.0009	32	0.0003	312.9	0.000
S x DT	2	0.0035	0.0017	32	0.0003	0.40	0.672
S x C vs.DT	1	0.0005	0.0005	32	0.0003	1.71	0.200
Site x all treatments	3	0.0050	0.0016	32	0.0003	5.35	0.004
Residual	32	0.010	0.0003				
Total	39	0.026					

except that 60 is slightly lower than 30 limpets. Percentage survival of *S.zelandica* in all density treatments was high (Figure 3.8). No treatment had less than 80% survival over time and there was not much difference between treatments. Survival was slightly better at Sharks Tooth than at Wairepo but this was only slight, an ANOVA showed that there was no significant difference in treatments or sites.

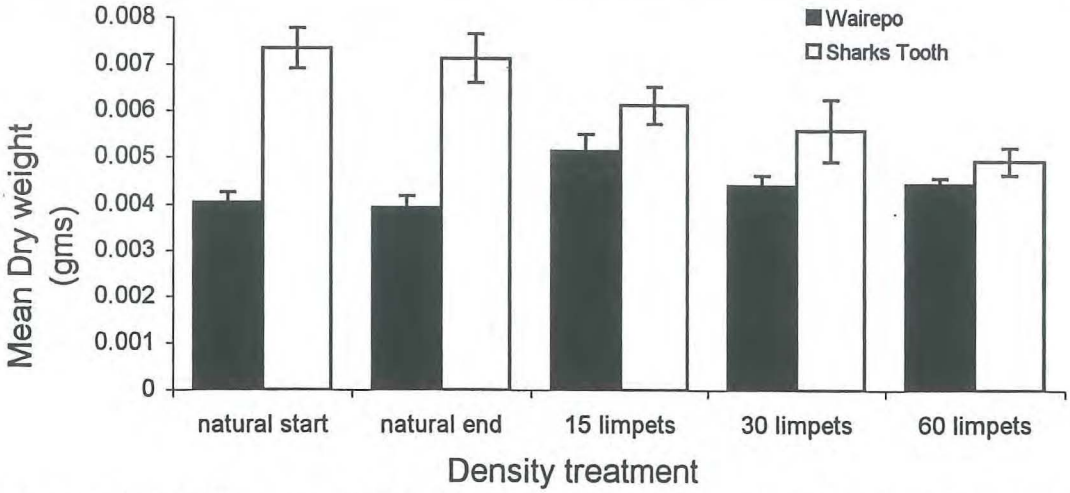


Figure 3.7: Mean dry weights (+/- S.E.) from the density experiment at Wairepo Flats and Sharks Tooth.

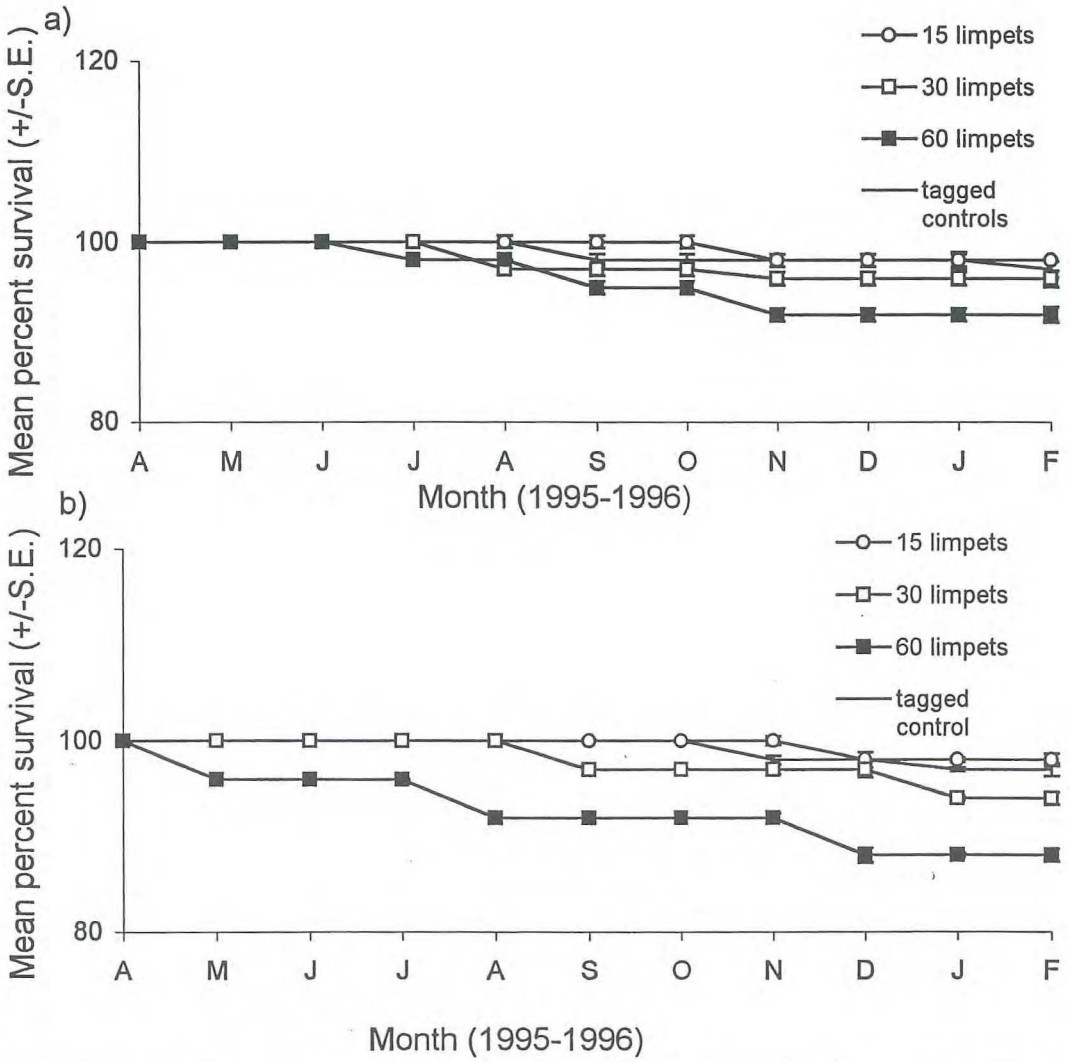


Figure 3.8: Mean percentage survival of *S.zealandica* in density experiment treatments at a)Sharks Tooth and b) Wairepo.

3.4 Discussion

Density of *S.zelandica* does have an effect on algal cover with double the normal density decreasing algal cover and total exclusion of limpets resulting in increased algal growth. In fact, there is pretty much a linear effect on algal cover of increasing density of limpets. This is a similar result to many overseas studies that found when limpets are removed there is a bloom of macroalgae, although it is generally accepted that the community that develops in the absence of limpets is not in a stable one (Farrell, 1988). Underwood and Jernakoff (1981) found that even high densities of *Siphonaria* species could not prevent algal growth. However, their study was based on the low shore where there is more wave splash and conditions are suited to quick algal growth. The present study was done on the midshore where algae is not so quick growing and *S.zelandica's* grazing effect is more noticeable. Although *S.zelandica* density did affect percentage algal cover, overall algal cover was more affected by season and algal succession than by *S.zelandica* grazing. Therefore, the general conclusions of Underwood and Jernakoff (1981) and Creese and Underwood (1982), that *Siphonaria* species are incapable of reducing algal cover to bare rock, hold true at Kaikoura. In this study the reduction of algae in summer is likely to be due to physical factors such as heat stress and desiccation rather than an increase in grazing. It is also due to the seasonal variation that naturally occurs in macroalgae (Beovich and Quinn, 1992). The fact that *S.zelandica* could not permanently reduce algal cover is not all that surprising when their feeding method is considered. They are known to crop macroalgae, leaving the basal parts of the plant intact (Underwood and Jernakoff, 1981). Therefore there will always be some macroalgae on the shore where there is predominantly siphonariid grazing.

There was significantly less algae at Wairepo than at Sharks Tooth, which may be a function of the fact that Sharks Tooth is the less sheltered site, receiving more wave action and less heat. Sharks Tooth also have a large seal population which may result in more localised nutrients at this site that are available for plants to utilise. The damper conditions mean that algae may

grow better and persist longer. The increased wave action at Sharks Tooth may also reduce limpet grazing as rougher conditions mean a greater chance of limpets being dislodged from the substrate, so grazing time will be reduced to decrease the chance of dislodgment. Within the density treatments at Sharks Tooth the percentage cover is generally what would be expected, with the sixty-limpet treatment having less algal cover over time than thirty limpets, which in turn had less algal cover than 15 limpets and 0 limpets had the most algal cover. The treatments stack up similarly at Wairepo Flats except that instead of the controls being similar to ambient density (30 limpet treatment) as at Sharks Tooth, they have the least amount of algal cover. This may be due to there being more large prosobranchs at Wairepo which could move into controls as they graze. Prosobranchs were not in abundance in the experimental area but they may move into the area while grazing. There are several potential reasons for the site differences. There are less strong currents in the Wairepo Flats site so there could be fewer algal spores brought into the area. Also there is the question of where the algae is recruiting from. Wairepo consists of long flat platforms and overall had less abundant algal cover compared to Sharks Tooth, therefore there are less adult plants to recruit from.

Results show a succession of algae similar to what has been found overseas (Sousa 1979, Underwood 1980,Cubit 1984). It has been reported before that *Siphonaria* species prefer *Syctosiphon* species as food (Beovich and Quinn, 1992). In this study *Syctosiphon* was the alga whose abundance was least affected. Instead it was found that *S.zelandica* significantly affected abundance of ephemeral green and red species such as *Ulva* and *Porphyra*. Gut analysis done on *S.zelandica* in 1985 (Raffaelli) found that red and green seaweeds made up the bulk of what was found, but Wong (1980) stated that *S.zelandica* actually feed on the microalgae found on macroalgae. It has been shown that *Ulva* species in New Zealand have a rich epiflora layer and no chemical resistance to grazers (McClatchie, 1979) which would explain why *S.zelandica* can keep the abundance of this algae down. *Porphyra* was minimal in all but

the exclusion treatment which indicates that this is an easily grazed item although it is very seasonal and not present for very long in the adult plant form. As this shows, algae is seasonal and although data shows it is obvious that *S.zelandica* can affect the distribution of the algae there are no real long term effects of *S.zelandica* on algal cover at Kaikoura. Therefore, the results of the treatments were real and *S.zelandica* probably contribute to the seasonal patch dynamics of the Kaikoura shore.

There have been some criticisms for using cage experimental enclosures as they can cause shading, reduce wave stress and trap debris (Cubit, 1984). However, the design of fences used in this experiment had no roof so there was no cover or shading effect from this and there were both half fence controls and open controls to investigate if there was any caging effect. The fences were checked once a week and debris cleared away, if there was any, so there was no chance for anything to accumulate. *S.zelandica* are crack-orientated in damp areas naturally so being inside a fence should not significantly change their survival or grazing patterns.

It is interesting that there is a treatment difference in the chlorophyll amounts as *S.zelandica* supposedly cannot graze on microalgae. The difference probably comes from the different densities of limpets. Where there is 60 limpets there may be less free substrate for algae to colonise. Chlorophyll levels showed a similar pattern to macroalgal abundance being greater in winter and autumn than in summer. However, unlike macroalgae, there was always some microalgae present. The dry weights of *S.zelandica* were reduced with increased density but not significantly, nor was mortality significant. In fact, mortality at Sharks Tooth was negligible while Wairepo it was slightly higher. As could be expected, the double density had the worst mortality but as it was still above 80% at the end of the experiment, increased density obviously did not cause a corresponding increase in mortality. Other studies have shown that *Siphonaria* species can tolerate adverse biological conditions for some time (Creese and Underwood 1982, Ortega 1985) and even thrive at higher densities (Burton, pers.comm.). From the results found in this study and

and overseas, it would appear that *S.zelandica* is very adaptable to different environmental conditions.

CHAPTER FOUR

Predation

PREDATION

4.1 Introduction

Predation is an important factor in regulating many intertidal populations (Paine 1971, Menge 1978, Menge et al.1994) and is the basis of identifying keystone species. It is also one of the most important interactions in complex trophic communities (Menge and Sutherland 1976, Garrity and Levings 1981). Predation interactions can be intricate as they can have effects beyond those on the predator and prey alone. Such effects can be indirect; for example, a reduction in grazer numbers on the shore by predator removing them, indirectly affects algal biomass, generally causing an increase in algal abundance. This in turn can affect grazer recruitment to an area (Wootton, 1992). Direct effects of predation are more obvious such as the increase in mortality of the prey species. These predation effects can sometimes be seen immediately, such as a decrease in the number of organisms on the shore, or may take time to be revealed, such as an increase in species diversity at the site (Menge and Sutherland, 1976).

There are many potential predators of limpets; two of the most widely studied are birds (Hartwick 1976a & b, Frank 1982, Hockey and Branch 1984, Marsh 1986, Wootton 1992) and whelks (Paine 1963, Menge 1978, Moran 1980, Branch and Cherry 1985, Barkai and Branch 1988, Iwasaki 1993). Predation of siphonariid limpets by fish (Cook 1980, Tablada et al.1994), whelks (Underwood and Jernakoff 1981, Creese and Underwood 1982, Iwasaki 1993), starfish (Feder, 1963) and birds (Hartwick 1977, Lindberg et al. 1987) has been specifically studied. However, predation of *Siphonaria zelandica* has not been studied although the whelk *Haustrum haustorium* has been observed to feed particularly on these limpets (Beckett 1968, Luckens 1974).

Hockey and Branch (1984),state that the effect of avian predation on intertidal community dynamics is not well understood. Wootton (1992) examined both direct and indirect effects of bird predation on limpets and algae through experimentation. He found that over the long term, indirect effects can "offset,

enhance or overshadow" the direct predation effect. He cautioned against drawing conclusions from directly observed effects of predation and stressed the importance of considering all biological and physical factors in studying a complete intertidal system. Generally oystercatchers as predators of gastropods have been well studied (Hartwick 1976a & b,1981, Frank 1982). However, the only study in New Zealand on oystercatcher predation is by Baker (1974), who made observations at three sites, including Kaikoura. He found that detection of prey was primarily visual and limpets larger than 40mm were rarely eaten. He also did population counts at Kaikoura and found that there were between one to two thousand birds in the area. Peak populations occur on the East Coast of the South Island in the summer months of January and February but the numbers vary seasonally. In the Kaikoura region the most common oystercatcher of the three species in New Zealand is the South Island Pied Oystercatcher (*Haematopus finschi*) (Plate 4.1). This bird has a distinctive black and white plumage pattern (Falla et al., 1981) and is closely related to the European oystercatcher. The other identifiable species that is occasionally found at Kaikoura is the Black oystercatcher (*Haematopus unicolor*).

On rocky shores in America and Britain up to 50% of the diet of oystercatchers is composed of limpets (Lindberg et al. 1987). Oystercatcher feeding rates are affected by competition with other shore birds such as gulls, which tend to be parasitic on the oystercatchers by stealing food that has already been located. Weather conditions are another limiting factor because oystercatchers feed only in calm conditions at low tides (Baker, 1974). To remove limpets from the rocks, oystercatchers insert their bill under the edge of the shell and then flick the limpets over, exposing the soft foot (Hartwick, 1976a). There are no studies on oystercatcher feeding rates in New Zealand but from northern hemisphere studies it appears oystercatchers can remove around one limpet per minute (Frank, 1982). From data similar to this, Lindberg et al. (1987) estimated that a flock of ten oystercatchers could remove between 600-1500

Plate 4.1: Pied Oystercatchers (*Haematopus finchsi*), centre, at South Bay in summer.

Marsh (1986) investigated avian predation on limpet populations in north-western America by using exclosure experiments. He found that excluding oystercatchers from large areas had no effect on the numbers of small limpets. However, larger limpets (19 - 30mm) had significantly decreased survival. Marsh also stated that bird predation caused changes in the behaviour of the limpets, although he gave no evidence of this.

Whelks drill the shell of their prey, eat only one animal at a time, and tend to feed for prolonged periods (Paine, 1963). *S.zelandica* is recorded as prey for *Haustrum* sp. in northern New Zealand (Beckett 1968, Luckens 1974). There are, however, some overseas studies that found whelks do not eat *Siphonaria* (Branch and Cherry, 1985) due to chemical and behavioural defences (Iwasaki, 1993). Defence against predation can take many forms; homing vs. non-homing behaviours(Branch and Cherry, 1985), shell shape (Palmer, 1979), chemical defence such as mucus (Branch and Cherry 1985, Tablado et al.1994) and movement or fleeing responses (Feder 1963, Garrity and Levings 1981). Defence can also be affected by height on the shore (Menge, 1978).

Siphonaria species overseas use several of these methods. Some home and their diurnal activity may be partly a defence mechanism. Possibly the most interesting is the secretion of a mucus that may be toxic. *Siphonaria* are rarely eaten compared to other limpet species (Iwasaki, 1993). *Siphonaria zelandica* has not been studied for defence mechanisms but has been observed to home (Jeffs, 1985) and to produce mucus.

The use of experimental enclosures to study oystercatcher predation on *S.zelandica* at Kaikoura was not considered. The mudstone platforms are 100m long and between 100-500m wide. *S.zelandica* occurs in patches on raised platforms within this area and the potential foraging area of oystercatchers is extensive. I considered that caging birds would be unlikely to yield a result. Oystercatchers in New Zealand occur in large, widely dispersed flocks (Baker, 1973). Numbers of oystercatchers at Kaikoura today are similar to what Baker found in 1973 with flocks of 30-100 birds (pers.ob). The aim of this study was to examine avian (oystercatcher) and gastropod (whelk) predation on *S.zelandica* at Kaikoura. Here I test the direct effect of whelk predation and if this is shore height dependant, as well as making observations on oystercatcher foraging habits.

4.2 Materials and Methods

Whelk Predation Experiment

This experiment had two objectives. The first was to determine if whelk predation affected the density of *S.zelandica* and the other was to determine *S.zelandica's* survival on the low shore compared to survival at the mid shore under natural predation. The experiment was done at Wairepo Flats. Ten complete cages and ten fences (i.e. cages without roofs) were constructed from Vexar™ mesh (Plates 4.2 & 4.3) of an area of 0.25m^2. These were attached to the substrate by nailing a piece of thin, flexible plastic (Plumbers tape™) using 30mm Ramset™ concrete nails and 40mm Ramset™ tappets at the corners. Elevated covers (that is a top with no sides) were also constructed. In this case holes were drilled in the substrate with a compressed air drill. They were then filled with epoxy resin that had a nylon Ramset rawl plug inserted into it and left for one day to harden. Each plastic mesh roof had a small (2cm) piece of Plumbers' tape™ superglued to each corner through which a screw was passed. This screw was then screwed into the rawl plugs in the substrate giving a height of 5cm from the substrate. The reason for the fence treatments being included was to control for shading effects and caging effects. The experimental layout was replicated at mid and low intertidal areas with the limpets at the low shore being transplanted from the mid-shore area. There is bare rock beneath the canopy of *Hormosira* plants on much of the lower shore. Transplanting was needed because *S.zelandica* are not normally found in the low shore algal area. The species of whelk used in the cages was *Haustrum haustorium*. A preliminary survey was done to count the number of whelks at low and mid shore using a 0.25m^2 quadrat. Five quadrats were sampled randomly every five meters along a tape running parallel to the shore at both heights and all whelks counted. This experiment was run for five months and monitored monthly by counting the number of surviving limpets and whelks in experimental area.

Plate 4.2: Complete 0.25m^2 predation experimental cage over *Homosira banksii* at low shore.

Plate 4.3: Complete 0.25m^2 predation experimental cage over bare substrate at mid shore with *S.zelandica* and coralline algae in cracks around the cage.

The treatments (Table 4.1) were complete cages with *S.zelandica* and whelks to test the predation effect of whelks, complete cages with *S.zelandica* only and half cages with the same treatments. The controls consisted of five open areas at mid shore and five at low shore marked in the corner by a 3cm strip of Plumbers™ tape. Another five open areas at mid shore served as controls for limpet transplantation

Table 4.1: Layout of whelk predation experiment done at Wairepo Flats; n=5.

Cage Type	Treatment	Area of Shore
complete	1 whelk & 30 transplanted *S.zelandica*	low shore
sides only	1 whelk & 30 transplanted *S.zelandica*	low shore
complete	30 transplanted *S.zelandica*	low shore
sides only	30 transplanted *S.zelandica*	low shore
roof control	transplanted (30 limpets)	low shore
open control	transplanted (30 limpets)	low shore
complete	1 whelk & 30 *S.zelandica*	mid shore
sides only	1 whelk & 30 *S.zelandica*	mid shore
complete	30 *S.zelandica*	mid shore
sides only	30 *S.zelandica*	mid shore
roof control	ambient density (27 - 33 limpets)	mid shore
open control	ambient density (27 - 33 limpets)	mid shore
transplant control	ambient density (27 - 33 limpets)	mid shore

The mean percentage survival of *Siphonaria* for each treatment at mid and low shore was plotted over time and analysed with ANOVA. Chlorophyll samples were taken from both mid and low shore treatments (for methods see Chapter Three) to determine the extent of microalgae available on the substratum between shore levels.

Bird Observations

In the summer of 1994/95 and 1995/96 bird observations were done at Wairepo and Mudstone sites as a result of earlier observations where numerous limpets were found upside down on the shore after oystercatchers had gone through

the area. Oystercatchers, which appear to be one of the main predators of *Siphonaria*, were observed through binoculars at low tides late in the day. A bird was arbitrarily selected and then watched for ten minutes, with the number of limpets flicked over by the bird counted. At the end of the ten minute period I investigated the area and counted the number of overturned shells on the rocks as a check of the reliability of the observations. These observations were carried out as often as tide and weather permitted which was at least once a month, over two summers. The number of oystercatchers was substantially less during the 1995/96 summer than in the previous year. Replicates varied on each occasion in the field due to varying number of birds being present but there were always at least five ten minute periods (i.e. five birds) in which birds were observed at each evening tide. The flock size was counted on each sampling date and number of flocks in the area recorded. *S.zealandica* patches in the area of bird foraging was measured, and the overall effect of bird predation was calculated.

4.3 Results

Whelk Predation

The number of surviving limpets in the low shore zone (Figure 4.1) was greatest in the open controls and roof-only controls. Closed cages with whelks in them had the least number of limpets in them at the end of the experiment and numbers decreased sharply from July to <5% surviving by November. The two fence treatments (with and without whelks) had very similar survival rates, dropping to 50% by September and 15% in November. The preliminary survey showed that the mean number of whelks in the mid shore were $3/m^2$ (+/-1) and in the low shore were $7/m^2$ (+/-2.3). *S.zelandica* that had been eaten by the whelks were obvious as a hole could be seen in the shell, those that had died due to other reasons had no hole in the shell. At the low shore shells with holes in them were counted to see if the limpets died due to predation.

At the mid tide zone (which is *S.zelandica*'s natural habitat) again the cage treatment including whelks had the lowest survival rates although the drop in numbers was not as rapid as for the low tide zone. The fence treatment including whelks also had quite low rates of survival finishing with only 20%. All other treatments and the controls were very similar, with none having less than 80% survival at the end of the experiment. When the number of drilled limpets that had been counted were taken off the total number surviving, the rate of survival is similar to that of limpets in the complete cage without whelk treatment (Figure 4.2).

An analysis of variance done on the final month's data (Table 4.2) showed that there was a significant difference between treatments (not controls), sites and in the site/treatment interaction. The treatment differences can be seen in Figure 4.3. The two treatments that included whelks show no difference in survival between sites and both have low levels of survival. However, the two treatments without whelks differ significantly between sites with the mid shore consistently having higher levels of survival. The controls also differ between sites in the same way that the fence/cage without whelks do but the two

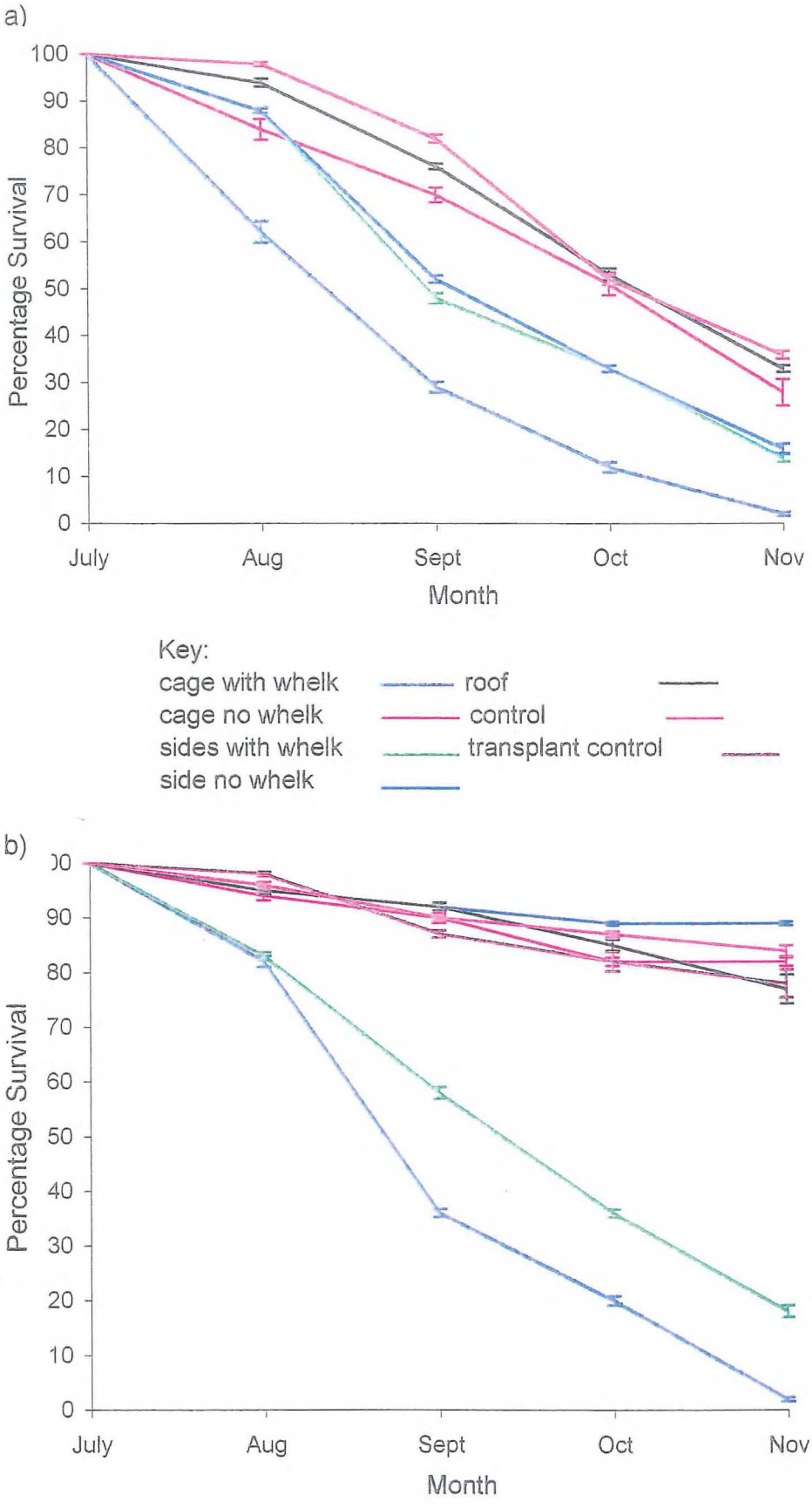


Figure 4.1: Number of surviving limpets over time for all treatments from the predation experiment at a) low shore and b) mid shore.

The lifted control at the mid shore site showed no difference in survival to the two other controls at this level. The number of whelks low on the shore in the preliminary survey was an average of eight in a $0.25m^2$ quadrat and on the mid shore it was only one per $0.25m^2$. The chlorophyll samples show a significant difference between mid and low shore (Figure 4.4) with there being some variation between treatments at both shore heights. However the treatment variation is not significant.

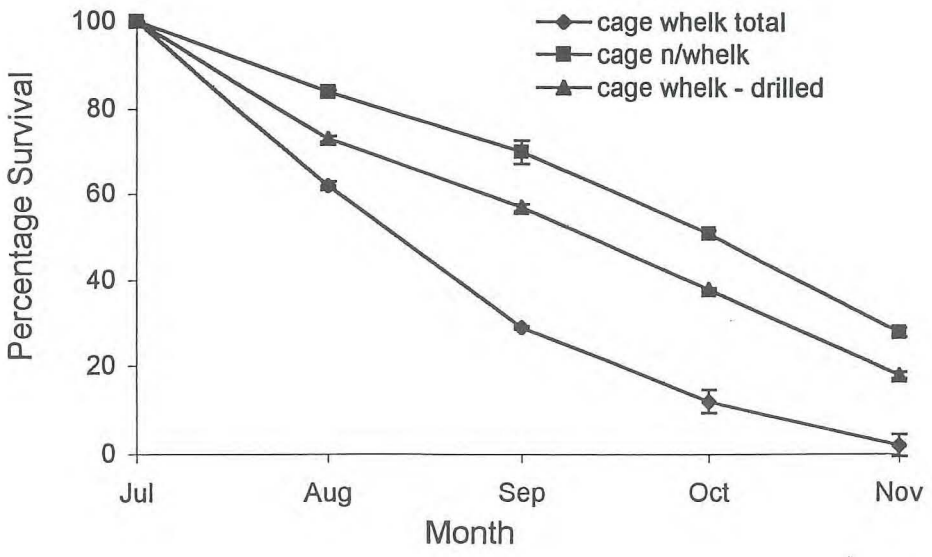


Figure 4.2: Percentage survival (+/-S.E) of complete caged limpets at low shore showing mortality due to predation and due to height on shore from July to November 1995.

Table 4.2: Analysis of Variance for numbers of surviving limpets at Wairepo Flats in November 1995. Variances homogeneous, (Cochrans test, p>0.05).

Source	df	SS	MS	F	p
Control vs. treatments	1	598.2	598.2	26.97	0.000
Between controls	1	138.6	138.6	2.68	0.090
Between treatments	3	1894.8	631.6	10.92	0.000
All treatments + controls	5	2631.7	526.3	47.92	0.000
Site	1	1760.4	1760.4	160.2	0.000
Site x treatments	3	877.6	292.5	40.14	0.000
Site x controls	1	0.800	0.800	0.435	0.000
Site x treatments vs.controls	1	29.03	29.03	66.92	0.000
Site x treatment/control interaction	5	907.4	181.49	16.52	0.000
Residual	48	527.18	10.98		
Total	59	5826.8			

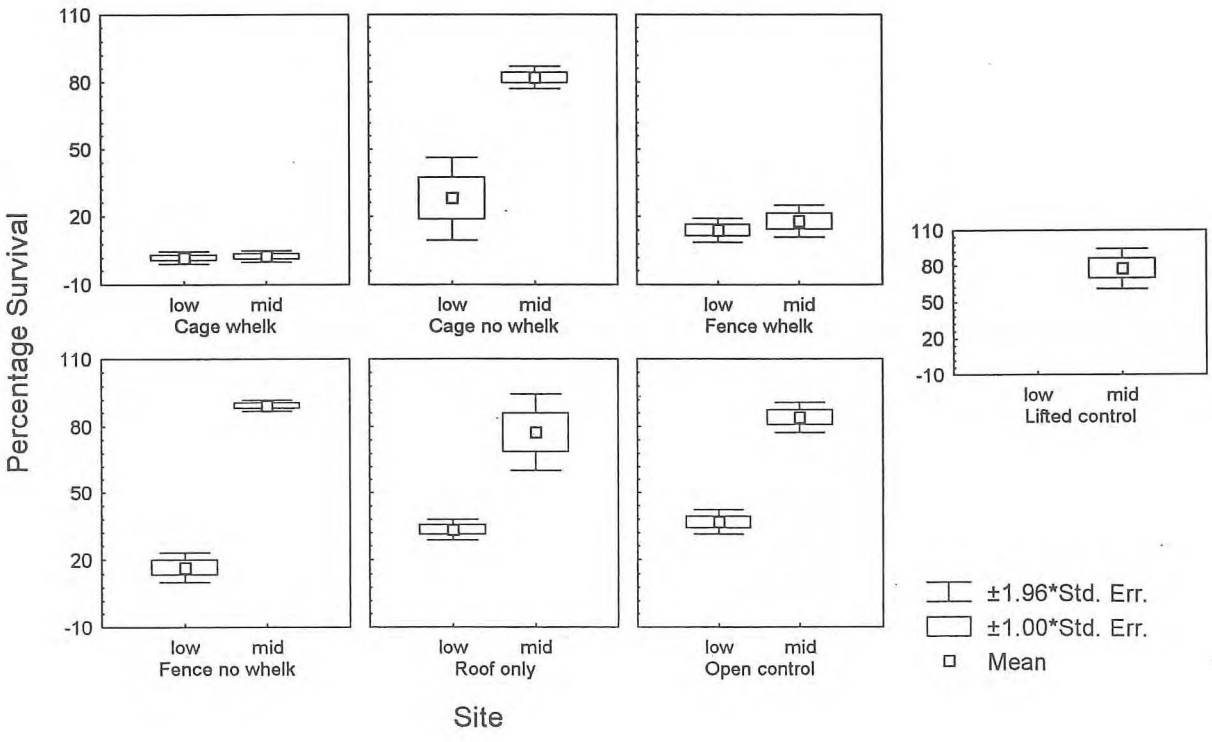


Figure 4.3: Box and whisker plot for mean percentage of *S.zelandica* surviving between treatments and sites, November 1995.

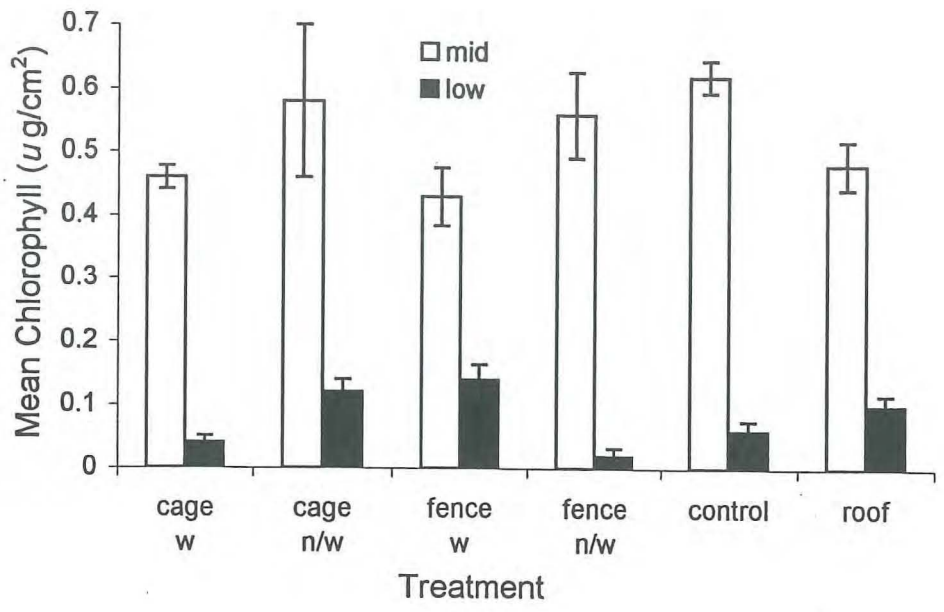


Figure 4.4: Mean chlorophyll levels (+/-S.E) at mid and low shore for all treatments in the predation experiment in July 1995.

Bird Observations

Oystercatchers did not eat any of the *S.zelandica* turned over but were seen attempting to eat the limpets. Figure 4.5 shows the mean number of limpets removed for each sampling date. An average of six birds were sampled on each date. The average number of limpets overturned per bird from the 1994/5 summer of 12.8 (+/-3) was similar to that the average for 1995/96 (11.5 limpets per bird, +/-3). The numbers of birds on the shore do vary but oystercatchers are always seen feeding in pairs or flocks. In the summer of 1994/95 there were between three and six flocks in Mudstone Bay were the sampling was carried out (Table 4.3). These flocks varied in size from between 18 to 40 birds. In 1995/96 there were fewer flocks, between 1 and 5, but bird numbers in flocks were similar to the previous year, with an average of 24. Patches of *S.zelandica* were measured after observations were done. Patch size varied from 3.4m^2 to 6.2m^2, with the average area being 3.3 m^2 (+/-0.8) and containing around 480 limpets. In all cases the number of overturned limpets counted on the rocks was the same as the number of limpets flicked off as seen through the binoculars. Therefore oystercatchers can remove an average of 1.8 limpets

per min. Using the *S.zelandica* patch sizes and the foraging rates of the oystercatchers, on average a flock of oystercatchers will remove 90% of a population of *S.zelandica* in one tidal cycle.

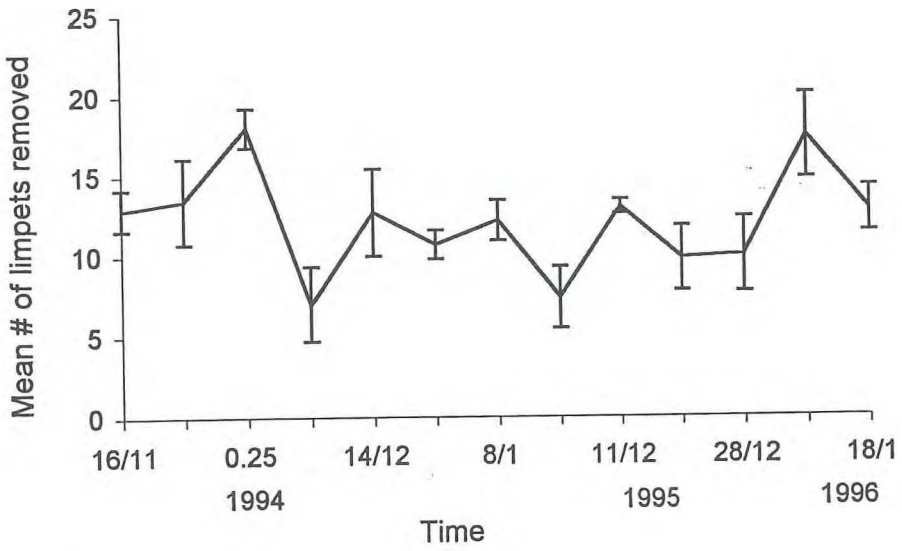


Figure 4.5: Mean number of limpets removed (+/-S.E) per bird, on each sampling date from November 1994 to January 1996.

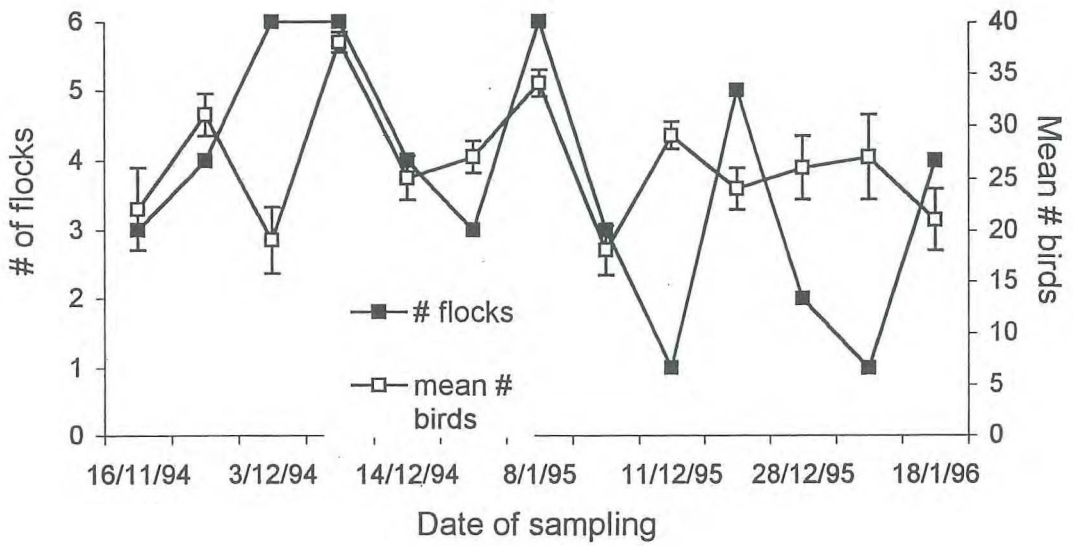


Figure 4.6: Mean number of birds per flock (+/-S.E), and number of flocks on each sampling date from November 1994 to January 1996.

4.4 Discussion

Whelk inclusion treatments showed that *Haustrum haustorium* has a significant effect on *S.zelandica* densities. In all whelk treatments the survival rate was low. In a natural situation whelks do not necessarily consume large numbers of limpets in a short time frame and results may have been enhanced by *S.zelandica* being the only available prey item. The fact that *Haustrum* does feed on *S.zelandica* is interesting in itself. Several studies done outside of New Zealand have found that other species of *Siphonaria* secrete a toxic mucus and are not eaten by whelks (Iwasaki 1993, Tablado et al.1994). In one study whelks in the field were repelled by *S.capensis* releasing a stream of mucus. The whelks would only feed on the limpets if they were damaged and unable to produce mucus (Branch and Cherry, 1985). *Siphonaria zelandica* does produce a milky-coloured mucus but it is obviously not toxic to *Haustrum* species. Homing has often been considered a defence against predation, although in a study of *S.sirius* which did home, the limpet still showed a fleeing response to whelks. *S.zelandica* is known to home (Jeffs, 1985) and does so at Kaikoura. It is not all that likely to be a defence against whelk predation as *S.zelandica* is also crack orientated and whelks prefer this kind of habitat.

In some locations predators are better at controlling prey densities in less harsh physical conditions (Menge, 1978). Whelks get less stressed in damp, shaded areas such as in crevices and are more likely to consume prey found in this kind of environment rather than going in search of food in harsher environments. This can lead to some of the problems in experimental design as discussed by Underwood and Denley (1984). They suggest that if environmental stress affects a predator, then a situation where the predator is confined to a cage can artificially change the environment. This leads, in the case of whelks, to increasing dampness in a cage making it similar to crevices so the rate of predation could be overestimated. The suggestions Underwood and Denley make to combat these problems - that is, having independent, separate treatments and using fences enclosing an area to eliminate artificial

shading - were already incorporated in the experimental design, so the prospect of an artificial environment in this experiment is unlikely.

At the mid shore zone, *S.zelandica* survived well in all treatments except those including whelks, yet at low shore all treatments had relatively poor survival. *S.zelandica* do not naturally occur at this level, and their reduced survival may be because of the lack of macroalgae for them to feed on. Another reason *S.zelandica* may not have survived is that the low shore is more exposed to wave action and they are more likely to be dislodged as they have a weak grip on the substrate but this would be unlikely on platforms. The difference in whelk numbers at low and mid shore shows they prefer the low shore area amongst the Hormosira. The difference in numbers of whelks also explains why there is greater predation at low shore rather than mid. The chlorophyll level in the low shore treatments was minimal which may have contributed to *S.zealandica*'s poor survival as they had nothing to feed on. However, the difference in numbers of limpets drilled and number that died naturally showed that there is a predation effect at low shore. This predation effect interacting with the limitation of food, combine to make the low shore an unfavourable habitat for *S.zelandica*, showing that biological processes can be a factor limiting the lower distribution of this species.

There is no doubt that oystercatchers remove large numbers of *S.zelandica* in a small time period and they must therefore significantly affect the density of these limpets. The seasonal occurrence of oystercatchers is concentrated in summer. Effects can be extensive; one bird removed 110 limpets in an hour and generally a flock only leaves 10% of limpets in a patch. This predation leads to localised changes in abundance. There are uneven effects of predation around the shore because oystercatcher foraging is so patchy. The localised reduction in density of limpets may lead to many of the indirect effects discussed earlier such as causing an increase in algal biomass or in space for sessile invertebrates to settle although I found no evidence of this. There is no obvious reason why oystercatchers overturn so many *S.zealandica* without eating them. In studies on northern hemisphere oystercatchers there is some

debate as to the preferred size of prey but in general they prefer limpets between 9mm and 20mm (Hartwick 1976 & 1981, Marsh 1986, Hahn and Denny 1989). *S.zelandica* fall into this size range so it may be that the birds are detecting their prey primarily visually. Or it could be that there are mainly juvenile birds present around the peninsula that are naive about prey items. This would explain why oystercatchers often attempt to eat *S.zelandica*. The mucus that *S.zelandica* produces may be toxic to birds and the main reason why oystercatchers never eat them. If they are adult birds that are removing these limpets it would seem a waste of time and energy. If oystercatchers are detecting prey visually, they may be confusing *S.zelandica* with Notoacmea species or with juveniles of edible prosobranch species. Other reasons for oystercatchers targeting *S.zelandica* are that oystercatchers apparently only attack limpets displaying a gap between their shell and the substrate (Baker, 1974). *S.zelandica* are frequently found in damp areas with their foot protruding below the shell.

Homing in *S.zelandica* may be an adaptation to avian predation as it would be harder to dislodge a limpet that is tightly clamped to the substrate with no openings around the edge. Another factor in oystercatcher predation is that they can only access prey on flat platforms (Marsh, 1986). *S.zelandica* occur mainly on such platforms and although they are crack orientated, they are easily accessible.

It would be of value for future work to look at the chemical components of the mucus produced by *S.zelandica* to determine its role as a defence mechanism, and for there to be more longterm studies on bird predation as it has been emphasised (Wootton, 1992) that short term predation studies cannot predict any longterm effects. Although it is clear that there are predation processes at work in this community, predation estimates are notoriously difficult to reconcile to actual events in nature (Branch, 1985). Results from this work would

indicate that both avian and gastropod predation are a major source of mortality and significantly reduce the density of *S.zelandica*.

CHAPTER FIVE

General Discussion

GENERAL DISCUSSION

Localised perturbations to *S.zelandica* populations cause indirect and direct changes in the mosaic of the Kaikoura shore. *S.zelandica* is patchy in distribution which appears to be not only a function of recruitment and settlement patterns but also due to predation pressure. Oystercatchers have a major seasonal influence on the abundance of *S.zelandica*, removing up to 90% of a population. This leads to an increase in space availability and causes less grazing pressure in this area of the shore. Indirect effects such as these have not been quantified and it is difficult to do so (Menge, 1995) but they are plausible outcomes of oystercatcher effects. The direct effect of grazing was investigated in Chapter Three and this showed that a reduction in the number of *S.zelandica* present on the shore caused an increase in algal abundance. The variation over time of the number of limpets sampled in the distribution and abundance section is possibly due, in part, to this predation pressure.

S.zelandica have no method of defence against bird predation other than production of a mucus that may be toxic and homing to a recognised scar. However, oystercatchers exert strong pressure with their bill and can remove *S.zelandica* whether the limpets are on their home scar or not. Being crack orientated may also be a defence mechanism as it is difficult for oystercatchers to dislodge limpets from vertical surfaces (Baker, 1974). By living in crevices, *S.zelandica* is occupying whelks common habitat which may make them more susceptible to predation by whelks, especially at midshore where whelks normally avoid dry areas. Whelks play a role in limiting the lower distribution of *S.zelandica* but the availability of suitable food is also a limiting factor. Survival of *S.zelandica* on low shore was poor indicating they are limited in distribution to midshore level at Kaikoura. Whelks actually consume *S.zelandica* unlike oystercatchers. This means that either the mucus *S.zelandica* produces is only toxic to birds or that whelks are not affected by it. Although predation in both avian and gastropod forms affects the abundance of *S.zelandica*, it is mainly

the adult population that is affected. Recruits are highly cryptic and not visible until they reach about 4mm, which is about one to two months old. Whelks may be able to eat these juveniles but they are probably not at risk of being consumed by oystercatchers as the birds would not be able to detect the juveniles. Therefore patches of *S.zelandica* should persist so long as there is sufficient recruitment (Creese, 1988). Predation limits not only the abundance of the prey species but also the amount of time a limpet can spend grazing (Branch, 1986). Oystercatcher removal of *S.zelandica* may also indirectly affect whelks as the birds are removing a large numbers of possible food items from the environment.

In northern New Zealand *S.zelandica* are abundant on *Ralfsia verrucosa* although densities are not high (Jeffs, 1985) and are possibly a refuge species. In South America three species of Siphonaria were found to be refuge species (Garrity, 1984). At Kaikoura, *S.zelandica* are abundant year round occurring over large areas mostly devoid of macroalgae. Sheer numbers suggest *S.zelandica* are well established members of the Kaikoura intertidal community rather than being a refuge species. *S.zelandica* were observed to home in this study and in northern New Zealand (Jeffs, 1985). Homing has been proposed as a behaviour developed to combat several problems such as predation and avoidance of desiccation. Although homing was not tested in this study, the potential reasons for this behaviour may play a large role in the continued survival of *S.zelandica* in the midshore. Homing does play a role in spatial distribution, keeping limpets discrete distances apart.

The reproductive cycle of *S.zelandica* is similar to that of other species of Siphonaria. An extended spawning season means that the population is replacing itself constantly rather than relying on one reproductive burst. This extended season means that there is a greater chance of veligers surviving to settlement stage. It would also help to avoid seasonal predation and may optimise food resources by controlling the arrival of new animals without suddenly pressuring food resources. Fecundity increases with size which is

common for Siphonaria species. One of the main reasons organisms adopt a long spawning stage combined with having planktotrophic larvae is to produce more offspring with a greater chance of survival. This is a common strategy in marine gastropods (Mileikovsky, 1971). This study could not determine survival rates of the veliger stage or recruitment rates to the substrate. This is an important area of the life history of *S.zelandica*. The egg masses hatched successfully and it is unclear why the veligers did not survive or settle but it may be that a chemical stimulant needs to be present to induce settlement.

Growth and mortality of *S.zelandica* was not density dependent as they could tolerate an increase in density without a loss of weight. Food supply does not pose a problem for *S.zelandica* as an increase in limpet density did not significantly affect algal abundance. The feeding method of *S.zelandica* also helps to ensure that there is adequate food for *S.zelandica*, as the limpets only crop the macroalgae, leaving the basal parts intact (Underwood and Jernakoff, 1981). Although *S.zelandica* does not interfere with the appearance of macroalgae on the shore they do have some effect on abundance of certain species (*Ulva* spp. *Enteromorpha* spp. and *Porphyra* spp.). These algal species have thin cell walls and no morphological defences against grazers (Lubchenco, 1978). *S.zelandica* are obviously indiscriminate feeders of macroalgae with no clear food preferences as at Kaikoura they consume many species of foliose macroalgae, while in northern New Zealand *S.zelandica* were found only on an encrusting algal species. The ability to consume a wide range of algae is advantageous as *S.zelandica* are more likely to survive if there is a failure in the seasonal algal bloom and it may mean that these limpets survive in many different habitats. The main affect *S.zelandica* has on macroalgae is that the limpets occupy space that is then unavailable for the propagules of algae to settle on. Limpet exclusion treatments were all colonised quickly by abundant macroalgae, while treatments that contained limpets took longer to show any colonisation. The colonisation succession that was seen on the Kaikoura shore is similar to that documented for Australian and northern hemisphere rocky intertidal communities (Emerson and Zedler

1978, Cubit 1984, Beovich and Quinn 1992). The site differences in algal abundance found in this study show that even over short geographical distances there are many factors that can be different enough to causes changes in the local community structure.

Investigations into rocky intertidal communities have led to general conclusions being made about what the driving forces are in space partitioning, food availability and the reasons for the existence of species in their particular habitat (Paine 1971, Menge 1976, 1991, 1995, Menge and Sutherland 1976, Branch 1986, Menge and Olson 1990). Individual populations are the cornerstones of community structure (Paine, 1973) whether they are a simple population or one with more complex interactions. Disturbance of a population can produce often unpredictable results (Paine and Levin, 1981) regardless of the disturbance being minor or not. Direct and indirect effects on the populations of *S.zelandica* at Kaikoura were examined in this study through examining disturbance events and their consequences. My study showed that *S.zelandica* plays a role in space occupation, resource occupation and in providing a food source. Overall, *S.zelandica* are primarily governed by the `top down' effects of predation. As food supply is not a limiting factor, bottom up effects are less important in the life cycle of *S.zelandica* at Kaikoura.

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APPENDIX A

Embedding and Staining Procedure

Appendix A: Methodology for embedding and staining gonad sections.

1) Embedding Process - running time 5 hours and 17 minutes.

Bath	Reagent	Immersion time
1	70% ethanol	2 minutes
2	Pass	-
3	Pass	-
4	Pass	-
5	Pass	-
6	90% ethanol	30 minutes
7	100% ethanol	15 minutes
8	100% ethanol	15 minutes
9	100% ethanol	15 minutes
10	Toluene	1 hour
11	Pass	-
12	Paraffin wax	3 hours

2) Staining Process: procedure haematoxylin and eosin.

Bath	Reagent	Immersion time
1	Xylene	5 min
2	Xylene/100% ethanol (50:50)	1 min
3	100% ethanol	2 min
4	90% ethanol	2 min
5	70% ethanol	2 min
6	50% ethanol	2 min
7	distilled water	2 min
8	Ehrlich's haematoxylin	30 min
9	distilled water	0.10 sec
10	0.5% aq Hydrochloric acid	0.01 sec
11	running tapwater	10 min
12	50% ethanol	2 min
13	70% ethanol	2 min
14	0.5% eosin in 70% ethanol	3 min
15	70% ethanol	0.30 sec
16	90% ethanol	2 min
17	100% ethanol	2 min
18	Xylene/100% ethanol (50:50)	1 min
19	Xylene	5 min

APPENDIX B

Seasonal Growth Rates

Appendix B: Seasonal growth increment for tagged S.zelandica at Sharks Tooth and Wairepo.

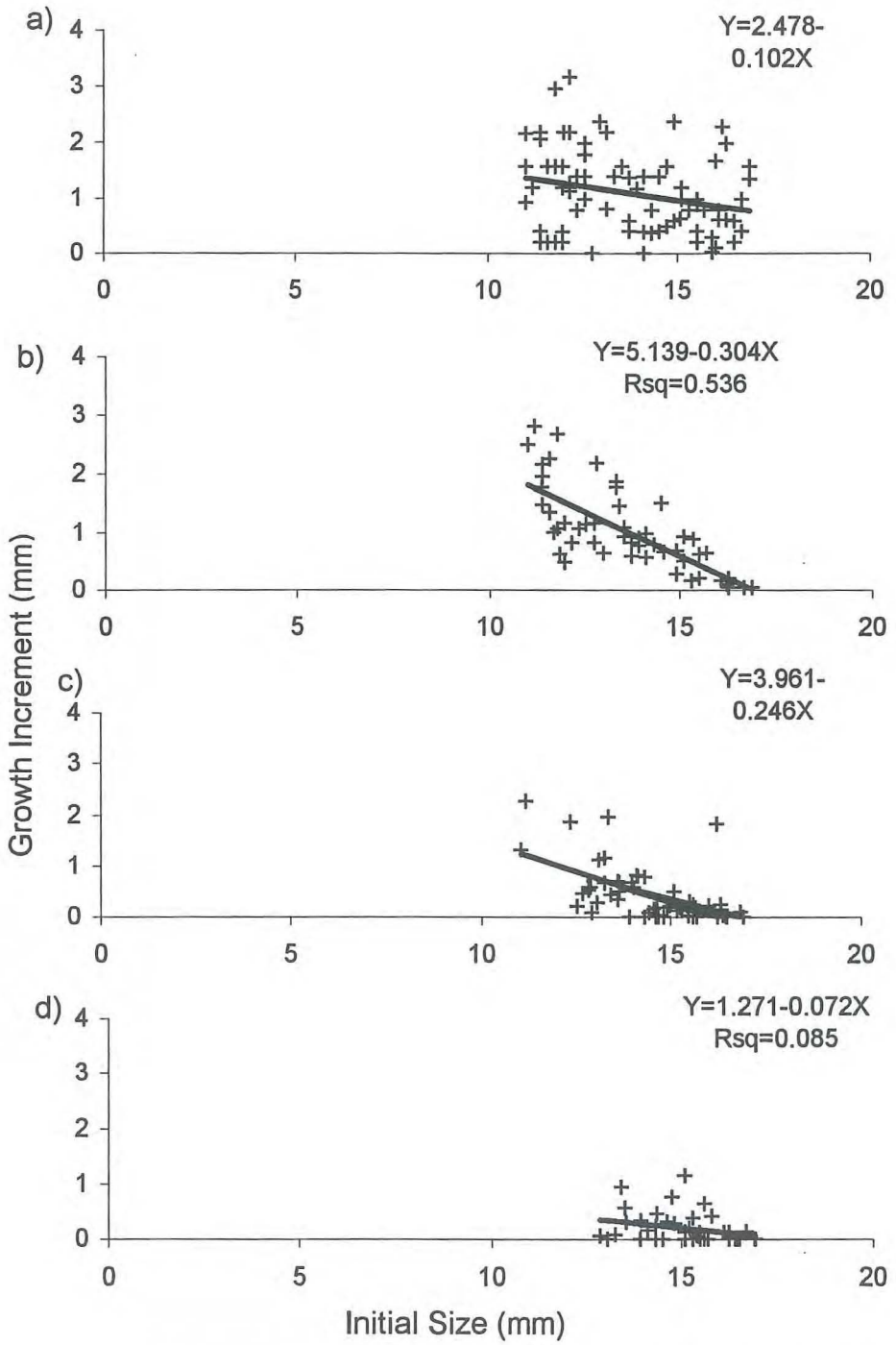

Figure B1: Seasonal growth increment for tagged *S.zelandica* at Wairepo Flats, **a)**autumn **b)**winter **c)**spring **d)** summ Regression lines, equations and R-square values are given.

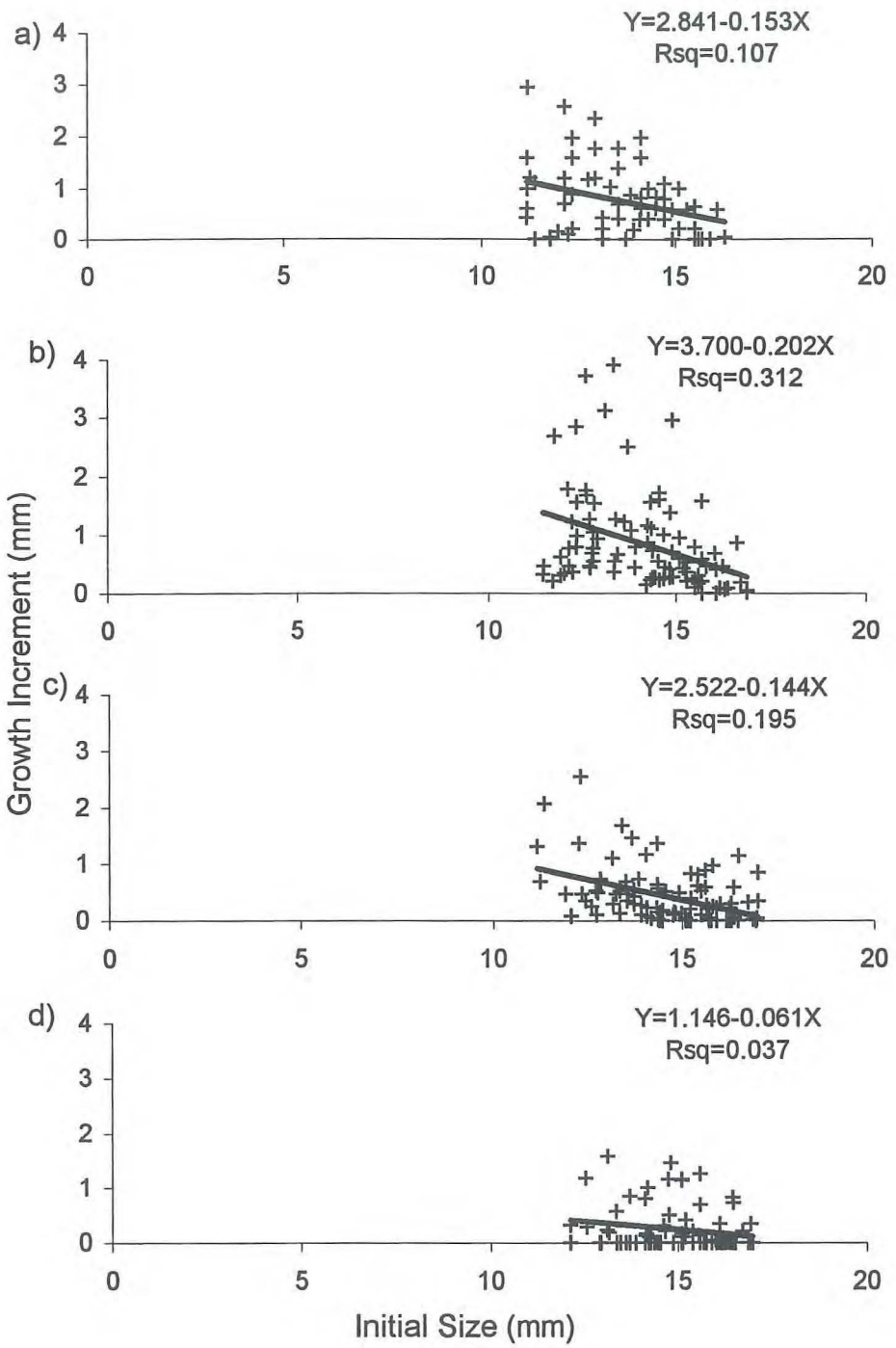

Figure B2: Seasonal growth increment for tagged *S.zelandica* at Sharks Tooth Point, **a)**autumn **b)**winter **c)**spring **d)** summe Regression lines, equations and R-square values are given.

APPENDIX C

Algal Species ANOVA and Box Whisker Data

Appendix C: Anova tables and box whisker plots for individual species of algae from the density experiment at their peak abundance.

a) *Syctosiphon lomentaria* - variances homogenous, (Cochrans test p>0.05).

Source	df	SS	MS	F	p
Between all T + C	5	3425.5	685.1	1.60	0.176
Between sites (S)	1	286.0	286.0	0.67	0.417
S x T	5	14457.4	281.4	6.77	0.000
Residual	48	20486.4	426.8		
Total	59	38655.3			

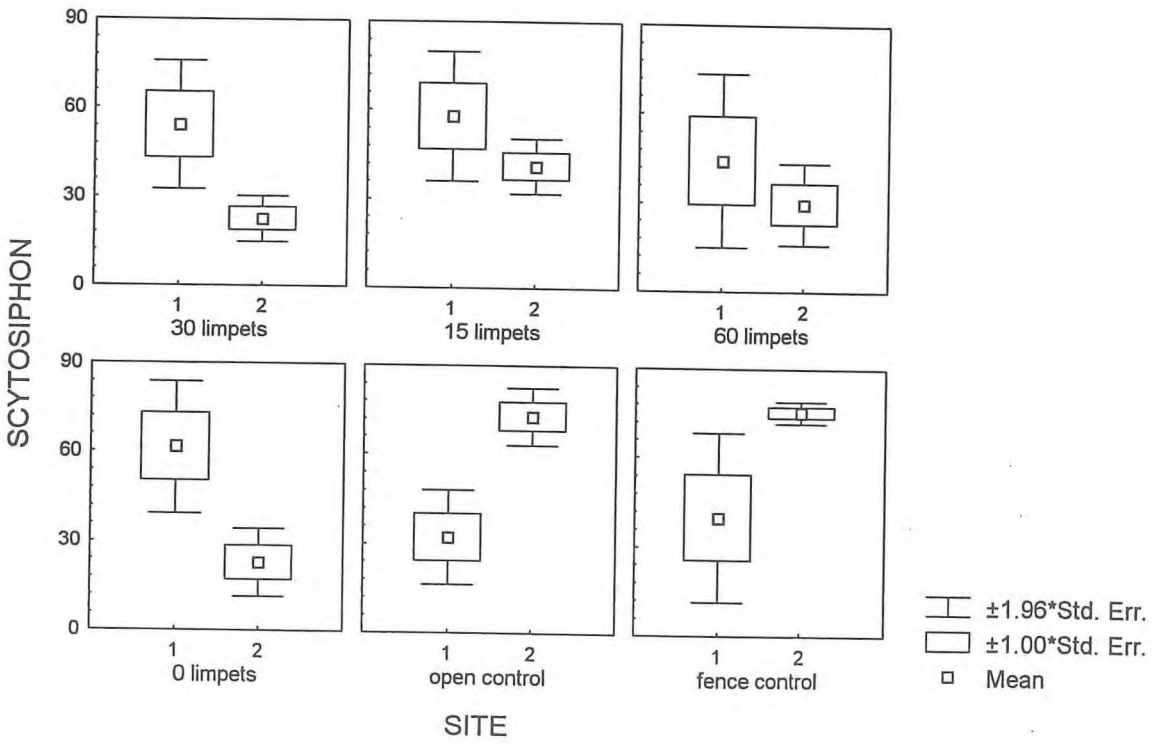

Figure C1: Box whisker plot for *Syctosiphon* at Sharks Tooth and Wairepo Flats showing differences in site and treatment in August 1995.

Table C2: *Porphyra* species - variances homogenous, (Cochrans test p>0.05).

Source	df	SS	MS	F	p
Between T + C	5	1493	298.6	1.40	0.238
Between Sites (S)	1	240	240.0	1.13	0.293
S x T	5	593.4	118.6	0.55	0.730
Residual	48	10190.4	212.3		
Total	59	12516.8			

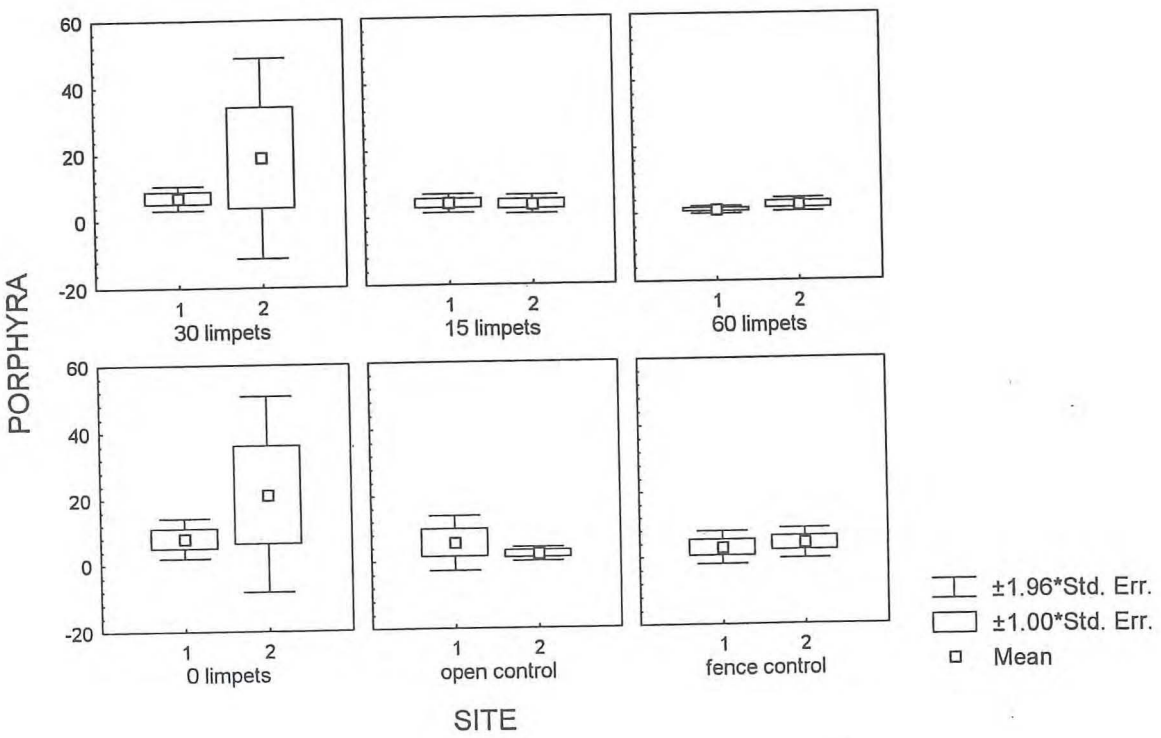

Figure C2: Box whisker plot for *Porphyra* at Sharks Tooth and Wairepo Flats showing differences in site and treatment in August 1995.

Table C3: *Ulva/Enteromorpha* - variances homogenous, (Cochrans test p>0.05).

Source	df	SS	MS	F	p
Between T + C	5	4439.5	887.9	3.516	0.008
Between Sites (S)	1	7020	7020	27.801	0.000
S x T	5	4420.2	884	3.501	0.008
Residual	48	12120.0	252.5		
Total	59	27999.7			

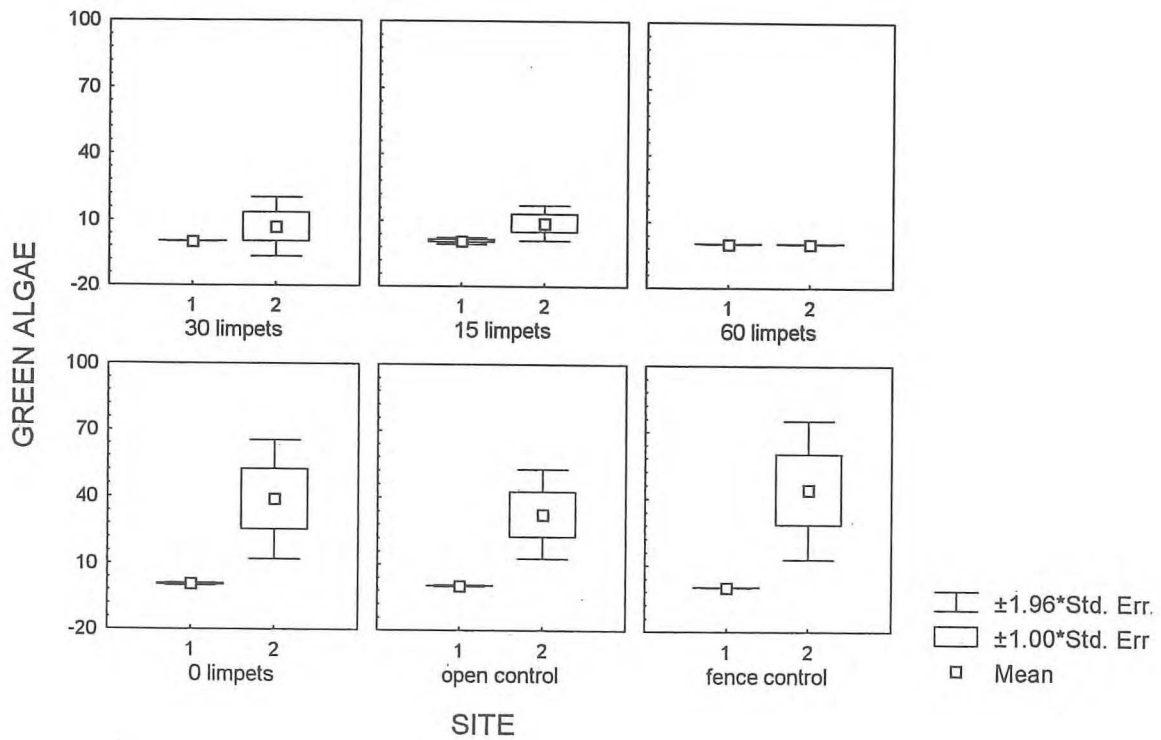

Figure C3: Box whisker plot for *Ulva/Enteromorpha* at Sharks Tooth and Wairepo Flats showing differences in site and treatment in August 1995.

Table C4: Algal film - variances homogenous, (Cochrans test p>0.05).

Source	df	SS	MS	F	p
Between T + C	5	8681.5	1736.3	3.192	0.014
Between Sites (S)	1	10773.6	10773.6	19.80	0.000
S x T	5	3797.8	759.5	1.396	0.242
Residual	48	26102.4	543.8		
Total	59	49355.3			

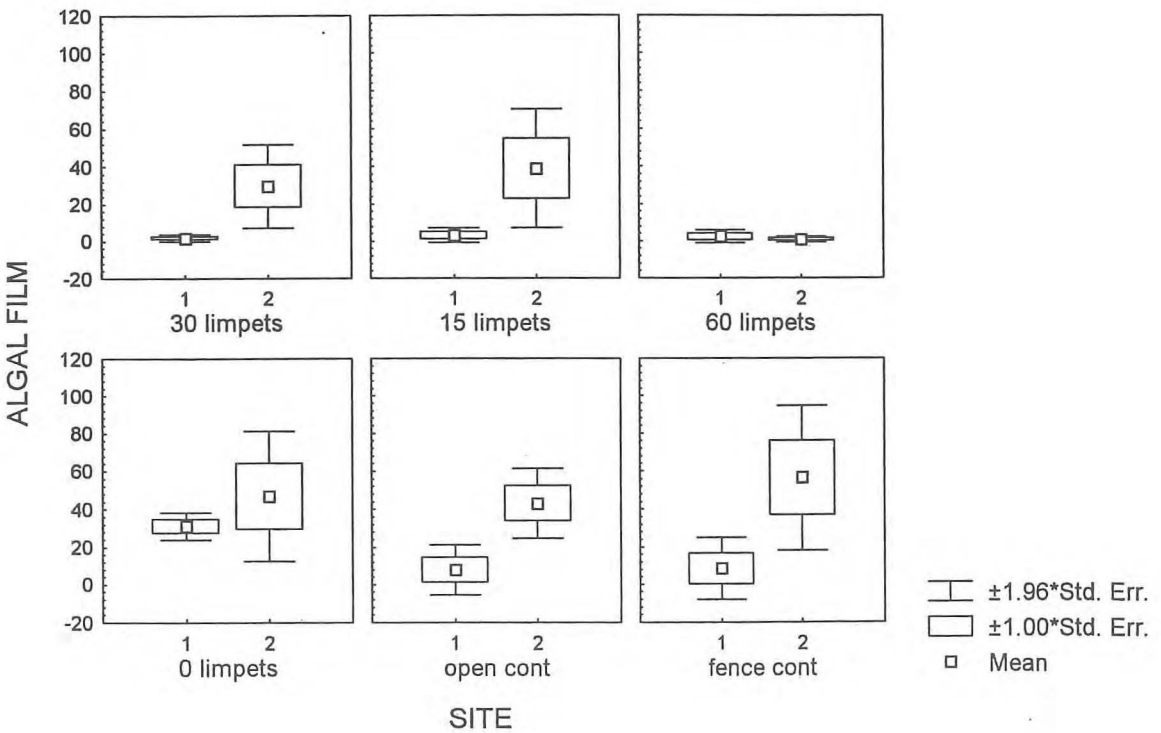

Figure C4: Box whisker plot for algal film at Sharks Tooth and Wairepo Flats showing differences in site and treatment in August 1995.